Palms

Journal of the International Palm Society Vol. 62(1) Mar. 2018

THE INTERNATIONAL PALM SOCIETY, INC.

The International Palm Society

Founder: Dent Smith

The International Palm Society is a nonprofit corporation engaged in the study of palms. The society is international in scope with worldwide membership, and the formation of regional or local chapters affiliated with the international society is encouraged. Please address all inquiries regarding membership or information about the society to The International Palm Society Inc., 9300 Sandstone St., Austin, TX 78737-1135 USA, or by e-mail to info@palms.org, fax 512-607-6468.

Bookstore: www.palms.org

Chapters: See www.palms.org

Website: www.palms.org

Palms (formerly PRINCIPES)

Journal of The International Palm Society

An illustrated, peer-reviewed quarterly devoted to information about palms and published in March, June, September and December by The International Palm Society Inc., 9300 Sandstone St., Austin, TX 78737-1135 USA.

Editors: John Dransfield, Herbarium, Royal Botanic Gardens, Kew, Richmond, Surrey, TW9 3AE United Kingdom, e-mail j.dransfield@kew.org.
Scott Zona, 6111 Twin Lake Drive, South Miami, Florida 33143 USA, e-mail scott.zona@yahoo.com.

Associate Editor: William J. Baker, Herbarium, Royal Botanic Gardens, Kew, Richmond, Surrey, TW9 3AE United Kingdom, e-mail w.baker@kew.org.

Guidelines for authors are available on request from the Editors, or on-line at:
www.palms.org/palms_author_guidelines.cfm

Annual membership dues are US$55.00 for Individuals (or US$150 for three years) and include a subscription to the Journal. Donor memberships are US$500 per year. Individual Lifetime memberships are available for a one-time fee of US$1000. Benefactor memberships require a one-time payment of US$2500. Subscription price is US$55.00 per year for libraries and institutions. Dues include mailing of the Journal by airlift service to addresses outside the USA. Dues may be paid on-line at www.palms.org.

Change of Address: Send change of address, phone number or e-mail to The International Palm Society Inc., 9300 Sandstone St., Austin, TX 78737-1135 USA, or by e-mail to info@palms.org.

Claims for Missing Issues: Claims for issues not received in the USA should be made within three months of the mailing date; claims for issues outside the USA should be made within six months of the mailing date.

Periodical postage paid at Austin, TX, USA and additional mailing offices. Postmaster: Send address changes to The International Palm Society Inc., 9300 Sandstone St., Austin, TX 78737-1135 USA.

PALMS (ISSN 1523-4495)

Mailed at Lawrence, Kansas 15 Mar. 2018

The full text of PALMS is available on EBSCO Publishing's database.

This publication is printed on acid-free paper.

CONTENTS

Features

THE INTERNATIONAL PALM SOCIETY
Conserve. Learn. Grow.

FRONT COVER

Coccothrinax acuminata growing in white sand savannas near Cortés, Cuba. See article by Moya López & Méndez Santos, p. 42. Photo by Paul Craft.

BACK COVER

Ceroxylon quindiuense 57.1 m high, at Las Cruces, Tochecito, Colombia, September 2017. Sabina Bernal, Blanca Martínez, Lina Berlinger and Tobias Simonis as scale. See article by Bernal et al., p. 5. Photo by Rodrigo Bernal.

Coccothrinax acuminata growing in white sand savannas near Cortés, Cuba. See article by Moya López & Méndez, p. 42. Photo by Robin Crawford.

PALM NEWS

Katja Schulz

Paysandisia archon, the large, day-flying moth from South America that is now an invasive pest in Europe, threatens native populations of *Chamaerops humilis*, the European Fan or Dwarf Palm. A recent study by J. Ruiz et al. (Biological Invasions. 2017. https://doi.org/10.1007/s10530-017-1656-1) **examined the spatial distribution of *C. humilis* in Mallorca and how the distribution and density of the host palm affects the establishment and expansion of the *P. archon***. At the front lines of the invasion, the ability of the moth to find and attack the palm is density dependent, i.e. palms are more likely to be attacked when they are close to a neighbor that is attacked. The situation is different, however, in areas that have been infested by the pest for a long time. In these populations, the likelihood of attack is lower if a neighbor is already under attack. The authors speculated that this counterintuitive result may occur when the moth population is high and female moths fly farther away to seek out palms on which to lay their eggs. The authors also found that larger palms are more likely to be attacked than smaller palms. Palm sex had no effect on the probability of attack by *P. archon*.

Scott Zona

Readers may be interested in a new study of **how light, temperature and seed moisture content affect germination of *Euterpe precatoria* seeds**. The publication by C.R.X. Costa et al. (American Journal of Plant Sciences 9: 98–106. 2018. https://doi.org/10.4236/ajps.2018.91009) details germination trials of seeds dried to different moisture contents, under different temperatures and photoperiods. They found that, under light (16 hours per day), optimum germination occurred at 20–30°C (68–86°F); at a higher temperature (35°C), germination was inhibited. In constant darkness, the best germination occurred under temperatures of 20°C or 25°C or alternating temperatures of 20°C and 30°C (simulating a night/day fluctuation). Seeds were tolerant of being dried to 11% moisture content, but seeds retained greater viability at higher moisture contents.

In a forthcoming paper in the journal Planta, A. de Santana Lopes et al. (https://doi.org/10.1007/s00425-018-2841-x) report **the complete plastid genome sequence for *Acrocomia aculeata***. The genome was characterized regarding its gene content, structure and evolution. Their analyses revealed that more than half of all plastid protein-coding genes within the palm family are under positive selection (as opposed to neutral drift). The distribution of these positive signatures suggests convergent evolution of most sites, including genes involving in photosynthesis. They also found highly variable sites that will be useful for genetic studies of natural populations and in work aimed at domestication and breeding of *A. aculeata* as an oil crop.

Tarciso Leão

As this issue goes to press, we have received notice of a **new book from Timber Press by IPS member Jason Dewees**. The book, *Designing with Palms*, will be published shortly and will be reviewed in a future issue of PALMS.

The World's Tallest Palms

RODRIGO BERNAL
Jardín Botánico del Quindío, Calarcá, Quindío, Colombia

BLANCA MARTÍNEZ
Universidad Distrital Francisco José de Caldas, Bogotá, Colombia

AND

MARÍA JOSÉ SANÍN
Facultad de Ciencias y Biotecnología, Universidad CES, Medellín, Colombia

A review of the tallest non-climbing palms around the world reveals 52 species that reach up to 30 m, and only 19 species that reach 35 m or higher. Both the largest documented measurements and the largest number of records confirm the Quindío wax palm of Colombia, *Ceroxylon quindiuense*, as the world's tallest species in the family. The Caribbean *Roystonea oleracea* ranks second tallest, and the Malesian *Pigafetta elata* and *Pigafetta filaris* tie for third place.

Palms hold some remarkable records, like the largest leaf of the plant kingdom in *Raphia regalis* (Hallé 1977) and the largest seed in *Lodoicea maldivica* (Dransfield et al. 2008). In fact, palms include, together with bamboos, the largest of all monocotyledons. The Andean wax palms in the genus *Ceroxylon*, in particular the Quindío wax palm, *C. quindiuense*, have long been credited with the title of the tallest of all palms. However, other palm species around the world also reach remarkable heights, even though their large size is less renowned.

Here we present a review of the palm species recorded to reach the largest heights. We include only non-climbing palms, as the biomechanical constraints of a climbing stem are quite different from those of an upright stem. As a result, climbing palms, like rattans, often reach considerable lengths, often surpassing 40 m. The longest record for a rattan is a stem 185 m measured on *Calamus manan* (Tomlinson 1990).

We have included in this review only those palms reaching 35 m or more. In most cases, records are taken from the literature, and it is not always clear whether a given measurement includes the crown or refers only to the stem height. In either case, the difference in total height is ca. 3–4 m. Our own measurements of live palms include the crown, and they are based on photographs with a human scale standing at the palm's base. In order to minimize the distortion caused by the camera lens, the images are taken from a long distance, using a telephoto lens. As the lower portion of the scale is often hidden by irregularities in the terrain or by vegetation growing near the palm, we often use two rods 2 m long and place one of them upright and the other in an angle, so that the zero point can be easily located at the vertex formed by them (Fig. 1). We use the software ImageJ (imagej.nih.gov/ij/) to analyze the images.

Measurements based on photographs may underestimate or overestimate size, depending

1. The scale we use for measuring palm heights, e.g. the palm in figure 4. The rods are 2 m long, and the vertex formed by them marks the point zero. Photo by Rodrigo Bernal.

on the position of the camera in relation to the center of the palm's stem. In the two cases in which we have been able to compare measurements based on photographs with actual measurements of the same individual after it fell over, we have found that placing the camera at a height ca. ¼ of the palm's height (as can be done, for example on a steep slope) leads to a more accurate measurement, with an underestimation of about 2%.

Results

We documented 52 species (2% of the species in the family) reaching to 30 m or more, and only 19 species reaching 35 m or more. For the latter, detailed information is presented in Table 1. Height of very tall plants, as recorded in the literature and on herbarium specimen labels, is often based on a rough estimate made by collectors in the field. Estimates of this kind are misleading, particularly in taller individuals, and they are often prone to exaggeration. Therefore, they should be interpreted with care. However, in some instances botanists manage to measure palms with appropriate instruments or have access to felled or fallen palms directly on the ground, and these measurements become valuable sources of information.

Both the largest documented measurements and the largest number of records confirm the Quindío wax palm (*Ceroxylon quindiuense*) as the world's tallest species in the family, reaching up to 61 m. *Roystonea oleracea* (up to 57 m), native of the Caribbean and northeastern South America, ranks as second, and *Pigafetta elata* and *P. filaris* (to 50 m), native from Sulawesi to New Guinea, tie for third.

Most of the remaining species among the 19 record-holders (e.g., *Cocos nucifera, Mauritia flexuosa, Rhopaloblaste ceramica, Roystonea regia, Veitchia joannis*) reach heights of 35 m or more only exceptionally: their common size most often ranges between 20 and 25 m. In contrast, for the tallest species, *Ceroxylon quindiuense, Roystonea oleracea, Pigafetta elata* and *Pigafetta filaris*, heights of 35–40 m are common, and many individuals in a population may reach that size. Additional information on the tallest species is provided below.

Ceroxylon quindiuense, Ceroxylon ventricosum and *Ceroxylum ceriferum*

While crossing the famous Quindío Trail in the Andes of Colombia in 1801, Alexander von Humboldt and Aimé Bonpland collected specimens of a species of wax palm 58 m tall. When first presented to science (Bonpland 1804), this species, which they named *Ceroxylon alpinum*, was not only the tallest of all palms, but it was also the tallest of all known trees. The taller *Eucalyptus* from Australia and the giant *Sequoia* from the western United States were not discovered until later that century.

However, as pointed out by Moore and Anderson (1976), Humboldt and Bonpland failed to realize that there were two species along the Quindío trail, a taller and a smaller one, and they provided a description that was a mixture of them both. As it turned out, however, their herbarium specimen, preserved at the Muséum d'Histoire Naturelle in Paris, corresponds to the smaller palm, and therefore it is this species which bears the name they coined, *Ceroxylon alpinum*. Thus, the taller species, which Humboldt and Bonpland recorded to be up to 58 m tall, remained unnamed until 1858. In that year, the German botanist Herman Karsten coined the genus name *Klopstockia*, with two species, *K. cerifera* and *K. quindiuensis*, both of which he claimed to reach 61 m in height (200 ft). The genus *Klopstockia* was later transferred to *Ceroxylon*, and these species are currently named *Ceroxylon ceriferum* and *Ceroxylon quindiuense*.

2. An individual of *Ceroxylon quindiuense* 52 m tall at the Cocora Valley, Colombia, September 1988. Botanist Ximena Londoño as a scale. This palm has since died. Photo by Rodrigo Bernal.

3. Participants in the World Palm Symposium posing by a *Ceroxylon quindiuense* 47.5 m tall at the Cocora Valley in Quindío, Colombia, June 2015. This palm fell over in 2017, and was measured on the ground. Photo by Rodrigo Bernal.

Ceroxylon ceriferum and *Ceroxylon quindiuense* are closely related, and, together with *C. ventricosum,* they make up a species complex (Sanín & Galeano 2011) that ranges from Venezuela to northern Peru. Although we have seen some individuals of *Ceroxylon ceriferum* in the Sierra Nevada de Santa Marta in Colombia, that can be up to 35 m, most individuals we have seen are no taller than 25 m. On the other hand, records of specimens

4. The world's tallest living palm currently known, *Ceroxylon quindiuense* 59.2 m high, at La Carbonera, Tochecito, Colombia, September 2017. Sabina Bernal, Tobias Simonis and Lina Berlinger as scale. Photo by Rodrigo Bernal.

of *Ceroxylon quindiuense* 50–60 m tall are numerous. Thus, Karsten's record figure of 61 m no doubt refers to *Ceroxylon quindiuense*. At the same place where Karsten found his 61-m tall palm, the French botanist Edouard André felled and measured the tallest palm he spotted at the Quindío trail in Colombia in 1876, and found it to be 60 m (André 1879).

Galeano and Bernal (2010) and Bernal and Sanín (2013) illustrated a specimen, which has since died, from the Cocora Valley in Quindío, Colombia, that was 52 m tall in September 1988 (Fig. 2). In that area, there are still many individuals 40–47 m tall. The tallest one at that site, a spectacular palm 47.5 m high, dwarfed participants in the World Palm Symposium held in Quindío in June 2015, when they posed for a group photo (Fig. 3). That palm fell over around July 2017. In the meantime, several taller palms have been located in the Tochecito river basin, just across the Central Cordillera, close to where André measured his 60-m tall palm. The tallest we have recorded so far measured 59.2 m in September 2017 (Figs. 1, 4). Other extremely tall individuals are also common in this same area (e.g., Back Cover).

Bernal and Sanín (2013) estimated the age of tall palms in Cocora, many of them 40–45 m tall, to be between 139 and 169 years. The tallest individuals, measuring 61 m, are probably close to 200 years old.

In southern Colombia, *Ceroxylon quindiuense* is replaced by the closely related *C. ventricosum*, which ranges to southern Ecuador. We measured tall individuals of this species at Chillanes, Ecuador, in October 2012. The tallest one we recorded was 35 m tall (Fig. 5). Farther south, in northern Peru, *Ceroxylon quindiuense* appears again at Ocol, near the town of Chachapoyas. At this locality, we measured several individuals ranging between 26 and 37 m.

Thus, the populations of *Ceroxylon quindiuense* in Quindío and Tolima, in the Central Cordillera of Colombia, not only harbor the largest genetic diversity in the *quindiuense* complex (Sanín et al. 2017), but they also include the tallest individuals in the group.

Roystonea oleracea

This is another well-known giant, with individuals often being over 35 m tall. The tallest ever measured was recorded in the island of Trinidad by the English journalist and novelist Edward L. Joseph. While he was manager of an estate in 1825, "one of these graceful palms was felled contrary to my orders. I found the tree measured 187 feet [57 m], exclusive of its spire" (Joseph 1838). What did Joseph refer to by the term "spire," we do not know. It might be the whole crown, including the crownshaft, as interpreted by Zona (1996), the crown without the crownshaft, or just the spear leaf. In the most extreme case, if we add the size of the crownshaft and the leaves, this individual would have been probably close to 61 m tall.

Another individual of this species, measured on the ground in Barbados, was 40.8 m tall (Hughes 1750). One individual in cultivation at the botanical Garden in Rio de Janeiro measured 38.7 m when it was struck by lightning in 1972. It was 163 years old (Johnson 1976). Large stands of this species can still be found in the savannas of the Orinoco basin in Colombia and Venezuela, and near the mouth of the Approuague River, in French Guiana (Fig. 6). At these localities, palms appear to be 30–40 m in height.

Pigafetta elata and *Pigafetta filaris*

Pigafetta elata and *P. filaris* are the tallest palm species in the Asian tropics, where they sometimes reach 50 m in height (Dransfield et al. 2008). Because both species were regarded as one single species for a long time (Dransfield 1998), it is not clear if both species reach the same height. They are fast growing palms, and therefore, extremely tall individuals are probably not very old.

Caryota obtusa

Like *Ceroxylon*, this is also a species of montane rainforest, growing between 1400 and 1800 m elevation. It ranges from Myanmar to Vietnam and southern China and grows up to 40 m tall (Henderson 2009). It is also reminiscent of *Ceroxylon* in its gregarious and localized habit, and in the swollen stem that narrows to a slender neck at its top. Its inflorescence is among the largest ones in the palm family (Hodel 1998).

Livistona saribus

This species emerges above the 25-m tall forest canopy in Cambodia, and its unmistakable crown, reaching 35 m in height, is an indicator of evergreen freshwater swamp forest (Theilade et al. 2011). Elsewhere in South and Southeast Asia, it grows up to 40 m (Henderson 2009), although most individuals are usually smaller.

Exaggerated records

Records of extremely tall palms are often based on wrong appreciation or exaggeration. Thus,

opposite

5. An individual of *Ceroxylon ventricosum* 35 m tall at Chillanes, Ecuador, October 2012. Botanist Lauren Gardiner as scale. Photo by Rodrigo Bernal.

6. *Roystonea oleracea* near the mouth of the Approuague River, in French Guiana, May 2013. These palms are ca. 35 m tall. Botanist Ingrid Carolina Romero as scale. Photo by Rodrigo Bernal.

for example, Hughes (1750) dismissed claims by "writers of wonders," who reported individuals of *Roystonea oleracea* in the Lesser Antilles to be 300 ft (91.4 m) in height. As mentioned before, he found the tallest to be 57 m high. Equally dismissible is the figure of 60–80 m given by André (1878) for *Ceroxylon quindiuense* in the Andes of Colombia, an

Table 1. Palm species recorded to be 35 m or more in height.

Species	**Distribution**	**Height (m)**	**Reference**
Ceroxylon quindiuense	Venezuela, Colombia, Peru	61	Karsten 1858,
		60	André 1879
		59.2	this paper
		58	Bonpland 1804
		57.1	this paper
		52	Galeano & Bernal 2010
Roystonea oleracea	Lesser Antilles to NE Colombia	57	Joseph 1838
		40.8	Hughes 1750
		to 40	Zona 1996
		38.7	Johnson 1976
Pigafetta elata	N Sulawesi	to >50	Dransfield 1976
Pigafetta filaris	Moluccas to New Guinea	to >50	Dransfield et al. 2008
Caryota obtusa	S China to E India, Thailand, and S Vietnam	to 40	Hodel 1998, Henderson 2009 Pei et al. 2017
Livistona saribus	Cambodia to the Philippines and Sumatra	30-40	Hodel 1998, Henderson 2009
		40	Pei et al. 2017
		35	Theilade et al. 2011
Mauritia flexuosa	N South America	to 40	González-B. 2016
Saribus rotundifolius	SE Asia	to 40	Dowe 2009
Roystonea regia	Florida, Cuba	36.6	Small 1937
		to 30	Zona 1996
Syagrus sancona	W Venezuela to Bolivia	36.6	Humboldt et al. 1816
		36	Noblick 2017
		to 30	Henderson et al. 1995
Caryota kiriwongensis	Peninsular Thailand	to 35	Hodel 1998, Henderson 2009
Ceroxylon ceriferum	N Colombia to N Venezuela	to 35	M.J. Sanín, pers. obs.
Ceroxylon ventricosum	Ecuador	to 35	this paper
Cocos nucifera	Pantropical	to 35	Dowe 2010
Hydriastele costata	Australia, New Guinea	to 35	Jones 1984, Dowe 2010
Hydriastele ramsayi	Australia	to 35	Jones 1984
Livistona nitida	Australia	to 35	Dowe 2010
Rhopaloblaste ceramica	Moluccas to New Guinea	to 35	Banka & Baker 2004
Veitchia joannis	Fiji, Tonga	to 35	Zona & Fuller 1999

obvious exaggeration, as he himself later mentioned that he felled and measured the tallest palm he spotted, and found it to be 60 m (André 1879). Another exaggeration is probably Humboldt et al.'s (1816) figure of 36.6–45.8 m ("20–25 orgyalis") for *Syagrus sancona* in Colombia. Whereas the lower figure seems likely (although rare) for extremely tall individuals of this species, we have never seen any plant that might be even close to 40 m.

Why are these species so tall?

This is the most frequent question we are asked when we show people the giant individuals of *Ceroxylon quindiuense* in Colombia. Unfortunately, there is no simple answer to this question. Overall size is a poorly studied trait in plants, compared to the attention it has received in animals (Smith & Lyons 2013) and compared to other plant traits, such as seed size (Eriksson 2008) or leaf size and shape (Brown et al. 1991). However, body size plays a fundamental role in a plant's life strategy. How much to invest in building a stem that will resist mechanical stress? How much will be gained from accessing a surplus of light?

Palm stems have to resist mechanical stress and enormous weight without secondary xylem, and have to be supple enough to move with wind currents and strong enough not to break. The tissue organization of the stem, a rigid outer cylinder enclosing a spongy core, provides an optimal combination of stiffness and elasticity. The mechanical properties of the stem must allow the vascular system to transport water and nutrients up and down a 50 m or more stem. The anatomical and mechanical qualities of the stem of a palm are initiated in the establishment phase. As sieve tubes are not replaced, those produced in the early phases of stem development must remain functional throughout the palm's lifetime (Tomlinson 2006), often well over a century. Why and how have such tall stems evolved in a lineage of plants with these kinds of anatomical and mechanical constraints?

A study of functional trait distribution among New World palms (Göldel et al. 2016) shed some light on this issue. Median stem height of palm assemblages is high in disturbed landscapes with open canopies, driven by hot or dry current or glacial climates. This trend appears to occur also at the global level when just the uppermost tail of stem height distribution is considered: 17 out of the 19 tallest palms in the world thrive in open or disturbed habitats, whereas only the Melanesian *Rhopaloblaste ceramica* and *Veitchia joannis* are restricted to closed forests.

A correlation of high stems and disturbed habitats makes sense, as stouter stems provide more protection to the meristem (as in *Ceroxylon quindiuense*, see Sanín et al. 2013), whereas small bodies have more exposed meristems that are more vulnerable in disturbed and open environments. However, such correlation fails to explain the extreme height reached by some species that occur side by side with smaller ones, or the difference in size among species in the same genus that have similar habitat preference, as in *Ceroxylon*. Even *C. quindiuense* itself exhibits considerable variation in size, and only in the Central Andes of Colombia does this species reach the heights that rank it as the world's tallest palm. Time will show whether the tallest palms in the world will perform better in the midst of global climate change.

Acknowledgments

We thank the CNRS (France) and the European Union's FP7 Project 212631 PALMS (Palm Harvest Impacts in Tropical Forests) for funding field work in Ecuador, Peru and French Guiana, Lina Berlinger, Sabina Bernal, Lauren Gardiner, Ximena Londoño, Carolina Romero and Tobias Simonis for posing as human scales and farm owners for giving us access to their palm stands.

References

André, E. 1878. L'Amérique équinoxiale. Le Tour du Monde 36: 129–224.

André, E. 1879. L'Amérique équinoxiale. Le Tour du Monde 37: 97–144.

Banka, R. and W.J. Baker. 2004. A monograph of the genus *Rhopaloblaste* (Arecaceae). Kew Bulletin 59: 47–60.

Bernal, R. and M.J. Sanín. 2013. Los palmares de *Ceroxylon quindiuense* (Arecaceae) en el valle de Cocora, Quindío: perspectivas de un ícono escénico de Colombia. Colombia Forestal 16: 67–79.

Bonpland. A. 1804. Mémoire sur le *Ceroxylon*, nouveau genre de palmiers. Bulletin des Sciences par la Société Philomatique de Paris 3: 239, 240.

Brown, V.K., J.H. Lawton and P.J. Grubb. 1991. Herbivory and the evolution of leaf size and shape. Philosophical Transactions of the Royal Society B: Biological Sciences 333: 265–272.

Dowe, J.L. 2009. A taxonomic account of *Livistona* R.Br. (Arecaceae). Gardens' Bulletin Singapore 60: 11–175.

Dowe, J.L. 2010. Australian Palms: Biogeography, Ecology and Systematics. CSIRO Publishing, Collingwood, Australia.

Dransfield, J. 1976. A note on the habitat of *Pigafetta filaris* in north Celebes. Principes 20: 48.

Dransfield, J. 1998. *Pigafetta*. Principes 42: 34–40.

Dransfield, J., N.W. Uhl, C.B. Asmussen, W.J. Baker, M.M. Harley and C.E. Lewis. 2008. Genera Palmarum: the Evolution and Classification of Palms. Kew Publishing, Royal Botanic Gardens, Kew – International Palm Society – L.H. Bailey Hortorium, Cornell University.

Eriksson, O. 2008. Evolution of seed size and biotic seed dispersal in angiosperms: Paleoecological and neoecological evidence. International Journal of Plant Sciences 169: 863–870.

Galeano, G. and R. Bernal. 2010. Palmas de Colombia. Guía de Campo. Editorial Universidad Nacional de Colombia, Bogotá.

Göldel, B., W.D. Kissling and J.-C. Svenning. 2015. Geographical variation and environmental correlates of functional trait distributions in palms (Arecaceae) across the New World. Botanical Journal of the Linnean Society 179: 602–617.

González-B., V. 2016. Los palmares de pantano de *Mauritia flexuosa* en Suramérica: una revisión. Pp. 45–83 in Lasso, C.A. et al. (eds.). Morichales, cananguchales y otros palmares inundables de Suramérica II. Colombia, Venezuela, Brasil, Perú, Bolivia, Paraguay, Uruguay y Argentina. Instituto de Investigación de Recursos Biológicos Alexander von Humboldt, Bogotá.

Hallé, F. 1977. The longest leaf in palms? Principes 21: 18.

Henderson, A. 2009. Palms of Southern Asia. Princeton University Press & The New York Botanical Garden, Princeton and Oxford.

Henderson, A., G. Galeano and R. Bernal. 1995. Field Guide to the Palms of the Americas. Princeton University Press, Princeton, New Jersey.

Hodel, D.R. (ed.). 1998. The Palms and Cycads of Thailand. Nong Nooch Tropical Garden, Thailand.

Hughes, G. 1750. The Natural History of Barbados. London. (available at www.biodiversitylibrary.org/item/101657#page/139/mode/1up)

Humboldt, F.W.H.A., A.J. Bonpland and K.S. Kunth. 1816. Nova Genera et Species Plantarum (quarto ed.). Vol. 1. Lutetiae Parisiorum: sumtibus Librariae Graeco-Latino-Germanico.

Johnson, D.V. 1976. Palm longevity. Principes 20: 70–71.

Jones, D. 1984. Palms in Australia. Reed Books PTY, Balgowlah, NSW, Australia.

Joseph, E.L. 1838. History of Trinidad. Henry James Mills, London. (available at https://books.google.com.co/books?id=GJNhmgEACAAJ&printsec=frontcover&source=gbs_ge_summary_r&cad=0#v=onepage&q&f=false)

Karsten, H. 1858. Florae Columbiae. Ferdinand Duemmler Successors, Berlin.

Moore, H.E. and A.B. Anderson. 1976. *Ceroxylon alpinum* and *Ceroxylon quindiuense* (Palmae). Gentes Herbarum 11: 168–185.

Noblick, L.R. 2017. A revision of the genus *Syagrus* (Arecaceae). Phytotaxa 294: 1–262.

Pei, S., S. Chen, L. Guo, J. Dransfield and A. Henderson. 2017. Flora of China. (available at www.efloras.org).

Sanín, M.J. and G. Galeano. 2011. A revision of the Andean wax palms, *Ceroxylon* (Arecaceae). Phytotaxa 34: 1–64.

Sanín, M.J., F. Anthelme, J.-C. Pintaud, G. Galeano and R. Bernal. 2013. Juvenile resilience and adult longevity explain residual populations of the Andean wax palm *Ceroxylon quindiuense* after deforestation. PLOS ONE 8: e74139. https://doi.org/10.1371/journal.pone.0074139

Sanín, M.J., P. Zapata, J.-C. Pintaud, G. Galeano, A. Bohórquez, J. Tohme and M.M. Hansen. 2017. Up and down the blind alley: Population divergence with scant gene flow in an endangered tropical lineage of Andean palms (*Ceroxylon quindiuense* clade: Ceroxyloideae). Journal of Heredity 108: 288–298.

Small, J.K. 1937. Facts and fancies about our royal palm. Journal of the New York Botanical Garden 38: 49–58.

Smith F.A. and S.L. Lyons (eds). 2013. Animal Body Size. University of Chicago Press, Chicago.

Theilade, I., L. Schmidt, P. Chhang and J.A. McDonald. 2011. Evergreen swamp forest in Cambodia: Floristic composition, ecological characteristics, and conservation status. Nordic Journal of Botany 29: 71–80.

TOMLINSON, P.B. 1990. The Structural Biology of Palms. Clarendon Press Oxford, New York.

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

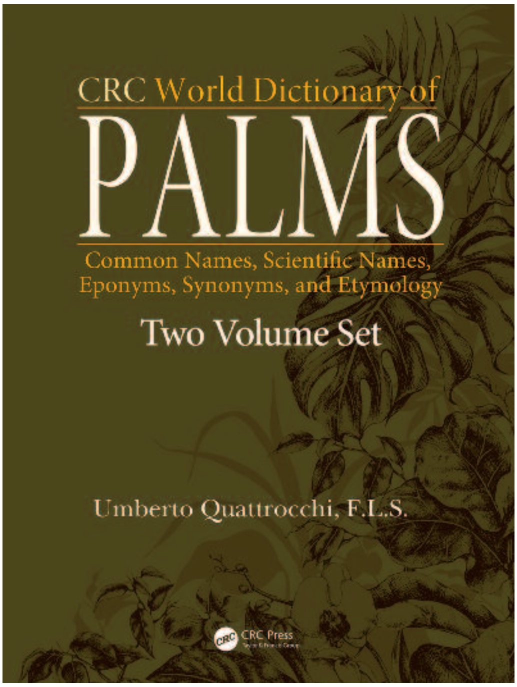
ZONA, S. 1996. *Roystonea* (Arecaceae: Arecoideae). Flora Neotropica 71: 1–35.

ZONA, S. AND D. FULLER. 1999. A revision of *Veitchia* (Arecaceae-Arecoideae). Harvard Papers in Botany 4: 543–556.

PALM LITERATURE

CRC WORLD DICTIONARY OF PALMS: COMMON NAMES, SCIENTIFIC NAMES, EPONYMS, SYNONYMS, AND ETYMOLOGY (2 Volume Set). Volume I Arecaceae A–G, Volume II Arecaceae H–Z, Cycadaceae, Zamiaceae, Cyclanthaceae. U. Quattrocchi. 2017. 3753 pages. ISBN 9781498782791. CRC Press, London, New York. Price $995.00/£636.00 (Hardback); $49.46/£35.99 (eBook).

This is an extraordinary compilation of information about almost all published species of palms, often reproducing protologues and complete descriptions, culled from the literature. That all this information is available in one place is surely a plus, but the cost of the extremely cumbersome hard copy volumes is exorbitant, and it leaves one to wonder who will ever be able to afford the work. It is available as an eBook, but I have not been able to see that in action. Inevitably such a work, once printed, rapidly becomes out of date. With free availability of on-line databases covering palm nomenclature and the existence of one partially complete database that covers nomenclature, taxonomy, distribution, ecology and uses (Palmweb, www.palmweb.org), much of the information in these two volumes is accessible via the internet (and inevitably more up to date). These databases also have links to illustrations (photos and scanned drawings).



Of course, much of the crucial historical literature is also available online via sites such as Google Scholar, Biodiversity Heritage Library and Jstor. This all leads one to wonder at the strangely outdated way of presenting these compiled palm data.

JOHN DRANSFIELD
Royal Botanic Gardens, Kew

TOMLINSON, P.B. 1990. The Structural Biology of Palms. Clarendon Press Oxford, New York.

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

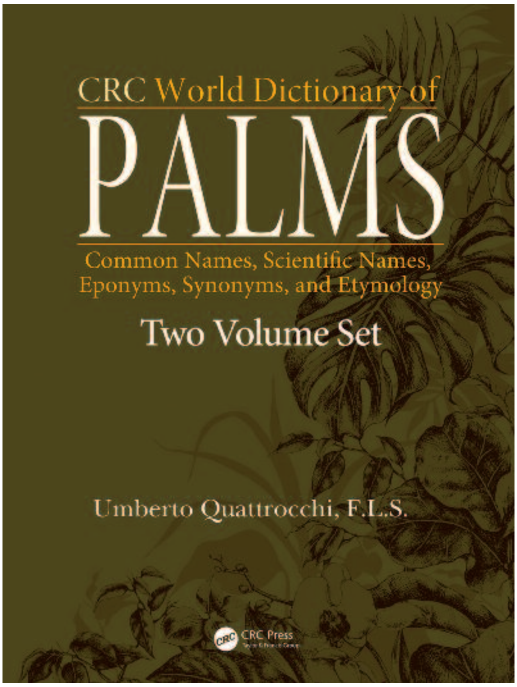
ZONA, S. 1996. *Roystonea* (Arecaceae: Arecoideae). Flora Neotropica 71: 1–35.

ZONA, S. AND D. FULLER. 1999. A revision of *Veitchia* (Arecaceae-Arecoideae). Harvard Papers in Botany 4: 543–556.

PALM LITERATURE

CRC WORLD DICTIONARY OF PALMS: COMMON NAMES, SCIENTIFIC NAMES, EPONYMS, SYNONYMS, AND ETYMOLOGY (2 Volume Set). Volume I Arecaceae A–G, Volume II Arecaceae H–Z, Cycadaceae, Zamiaceae, Cyclanthaceae. U. Quattrocchi. 2017. 3753 pages. ISBN 9781498782791. CRC Press, London, New York. Price $995.00/£636.00 (Hardback); $49.46/£35.99 (eBook).

This is an extraordinary compilation of information about almost all published species of palms, often reproducing protologues and complete descriptions, culled from the literature. That all this information is available in one place is surely a plus, but the cost of the extremely cumbersome hard copy volumes is exorbitant, and it leaves one to wonder who will ever be able to afford the work. It is available as an eBook, but I have not been able to see that in action. Inevitably such a work, once printed, rapidly becomes out of date. With free availability of on-line databases covering palm nomenclature and the existence of one partially complete database that covers nomenclature, taxonomy, distribution, ecology and uses (Palmweb, www.palmweb.org), much of the information in these two volumes is accessible via the internet (and inevitably more up to date). These databases also have links to illustrations (photos and scanned drawings).



Of course, much of the crucial historical literature is also available online via sites such as Google Scholar, Biodiversity Heritage Library and Jstor. This all leads one to wonder at the strangely outdated way of presenting these compiled palm data.

JOHN DRANSFIELD
Royal Botanic Gardens, Kew

Fruit Morphology and Yield of *Bactris gasipaes* in Tumupasa, Bolivia

VIVIANA VARGAS
Herbario Nacional de Bolivia,
c/27 Cota Cota s/n campus universitario,
Universidad Mayor de San Andrés, La Paz, Bolivia
vivianavargas130391@gmail.com (corresponding author)

MÓNICA MORAES R.
Instituto de Ecología,
Universidad Mayor de San Andrés,
Casilla 10077 -Correo Central,
La Paz, Bolivia
monicamoraes45@gmail.com

AND

JULISSA RONCAL
Department of Biology,
Memorial University of Newfoundland,
232 Elizabeth Avenue,
St. John's, NL A1B 3X9,
Canada
jroncal@mun.ca

The Bolivian indigenous group Tacana recognizes three varieties of the Neotropical widely cultivated *Bactris gasipaes* based on fruit color. Here we provide morphological differences among them and estimates of fruit yield for their sustainable management.

Bactris gasipaes Kunth, known regionally as *pejibaye* or *chontaduro* palm, is widely cultivated from Costa Rica to Bolivia for its palm heart, trunk and fruit (Mora-Urpí et al. 1997, Batista & Clement 2005, Clement 2006, Fig. 1). In Bolivia, it is locally known as *chima,* a name used for wild populations, which grow along riparian forests. The cultivated populations grow in secondary forests and fallow lands, between 140 and 800 meters of elevation, and are known as *tembé* (Moraes 2004a, Balslev et al. 2012).

The *chima* palm is very important to several ethnic groups, for whom it is a multipurpose palm (Macia et al. 2011, Moraes et al. 2015, Moraes et al. 2016a). For example, the Tacana people – among the best studied indigenous groups in South America (Cámara-Leret et al. 2014) – live in 20 communities surrounding the town of Tumupasa (La Paz department, NW Bolivia) and use this palm species to satisfy their food, medicine and shelter requirements (Moraes et al. 1995, Hissink & Hahn 2000, Paniagua-Zambrana et al. 2007). The hard, durable trunk is used to make bows and arrows, a 30 cm long tool used for weaving fabric and implements for fruit picking (Hissink & Hahn 2000, Díez Astete 2011). The palm heart and fruit are harvested as part of their basic diet, and indigenous healers use this species in rituals (Hissink & Hahn 2000).

The fruits of *B. gasipaes* are highly nutritious due to the presence of oleic acid, essential amino acids and most importantly, a high concentration of vitamin C and beta-carotene (Pasquel & del Castillo 2002, Bernal & Galeano 2013). Girón and Ordoñez (2016) found eight types of carotenoids in the fruit pulp with average concentrations up to 125.43 g/g. Furthermore, the pulp has a higher concentration of carbohydrates than either rice or potato (Saldias 1991). *Chima* fruits are eaten after being boiled with salt, are fed to animals and are processed into flour (Uglade & Pineda 2004, Goulding & Smith 2007, Moraes 2014b). In Bolivia, seeds are used for medicinal purposes; they are boiled for 8–12 hours until a dense oil is extracted, which is used to treat influenza and tuberculosis and to reduce fever (Moraes 2004b, 2014a). In western South America, this species is used for several other treatments (Paniagua-Zambrana et al. 2015).

Bactris gasipaes has two recognized varieties: the wild *B. gasipaes* var. *chichagui* (H. Karst.) A.J. Hend., and the cultivated *B. gasipaes* var. *gasipaes*. The two varieties differ with respect to fruit color, consistency, texture, size and shape (Clement 1986, Henderson 2000, Moraes 2004a, Batista & Clement 2005, Vargas 2014). Furthermore, the cultivated *B. gasipaes* var. *gasipaes* varies in terms of the density of spines and trunk length (Clement 1986). Clement (1986) considered fruit diameter, weight, brightness, exocarp color, and presence of stripes, as the most important fruit morphological characteristics for distinguishing among cultivated varieties.

1. Single stemmed palms of *Bactris gasipaes* in the lowlands of Tumupasa, Bolivia. Photo by Mónica Moraes.

Similarly, the Tacana distinguish the two varieties, variety *chichagui* and variety *gasipaes*, by using two vernacular names, *chima* and *tembé*, respectively. Local inhabitants of the Bolivian Amazon think that the cultivated variety was derived from hybrids between wild and introduced plants from Costa Rica and Peru (Saldias 1991, T. Cartagena, pers. com. 2014). The Tacana harvest three fruit types of *B. gasipaes*: yellow, orange (which is the putative hybrid) and red, referring to them as local varieties (Fig. 2). We have witnessed in the field that the Tacana exchange seeds based on the characteristics of mature plants in an attempt to maintain the wild populations that they know. Furthermore, the Tacana use seeds as currency for commercial exchange (Fig. 3), and seeds are given as gifts among the settlers.

In terms of fruit yield, Montúfar and Rosas (2013) found in western Ecuador that each adult tree of *B. gasipaes* var. *gasipaes* produced an average of 5–10 infructescences, each weighing up to 19 kg and bearing 75–400 fruits. The fruits were 1–9 cm in diameter and matured in three or four months (Montúfar & Rosas 2013). In Bolivia, Saldias (1991) conducted a study on production of *chima* fruits at Amboró National Park in Santa Cruz. He found that each palm produced 6–10

2. *Bactris gasipaes* varieties in Tumupasa, Bolivia. Red fruits (middle infructescence) belong to wild individuals, while yellow and orange-green fruits belong to cultivated individuals. Photo by Mónica Moraes.

infructescences, and that yield potential of fruits can provide information on the population structure of the species. Several other studies have been conducted across South America showing basic information on palm fruit harvest and management (Rivas & Barilani 2004, Bernal & Galeano 2013, Isaza et al. 2013).

Information on the population structure of palms can determine the current fruit harvest practice in a locality, which can be either destructive or sustainable (Rivas & Barilani 2004, Bernal & Galeano 2013). In order to formulate an adequate resource management for Tumupasa, Moraes et al. (2016b) conducted population evaluations of *B. gasipaes*. The population structure in an area of 1200 m^2 showed that the number of individuals decreased as they increased in age. The *chima* palm depends on the 85% of the regeneration stages (seedlings and juveniles) to support the development of adults (8.7%) and subadults (6%) (Vargas 2014, Moraes et al. 2016b). The population density was two to five adults in an area of 1,200 m^2. This structure corresponds to a sustainable population.

Since the *chima* fruit has both an economic and cultural importance for the Tacana, the aim of this work was to assess the production characteristics of *B. gasipaes* for its adequate harvest and sustainable management in areas surrounding Tumupasa. To achieve this, we characterized fruit morphological variation of local varieties and analyzed fruit yield potential.

Methods

Study site: Tumupasa is a Tacana town located 56 km north of San Buenaventura, Department of La Paz, Bolivia. The climate is tropical with an annual temperature or 19–33°C, and annual precipitation of 235–1000 mm (CIPTA & WCS 2005). According to Navarro and Maldonado (2002), this area belongs to the Amazonian district of Madidi, with evergreen forests on alluvial plain, sub-Andean hills and riparian forests.

Fruit morphology analysis: Three sites adjacent to Tumupasa were selected: Infierno, Mamuque River and Saint Lorenzo. On each site, we collected two or three ripe infructescences and measured the total number of fruits, number of rachillae, total mass and length (Clement 1986, Saldias 1991, Lozada & Moraes 2013). We studied eight infructescences in total, and from each of them we selected eight ripe fruits at random based on the finding of Manfío et al. (2011) that a minimum sample of four fruits is adequate for

3. Seeds of *Bactris gasipaes* used for commercial exchange among settlers. Photo by Mónica Moraes.

morphological analyses. We measured fruit diameter, length, and weight for a total of 64 fruits. We conducted an analysis of variance (ANOVA) followed by Tukey HSD post-hoc tests for all inflorescence and fruit variables to reveal differences among varieties.

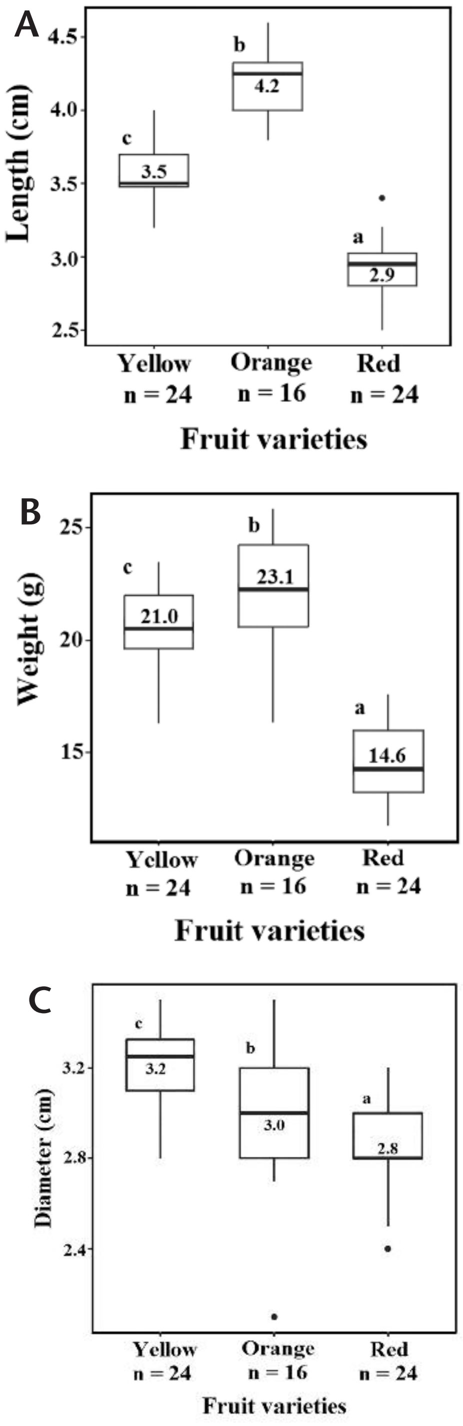
Yield analysis: Various formulas have been used to infer potential yield in palms, all of them are based on the average number of fruits per infructescence. For example, yield was estimated based on fruit weight and the number of infructescences per hectare (Velarde & Moraes 2008, Miranda et al. 2009, Lozada & Moraes 2013). In the present study, we used the following two formulas which were modified from Rivas and Barilani (2004) and Velarde and Moraes (2008): Yield in kg/ infructescence = (average weight (kg)/fruit) × (average #fruits/infructescence), and potential yield in kg/1000 m^2 = (average weight of fruits (kg)/infructescence) × (# infructescences/1000 m^2).

Results and Discussion

Since our sample sizes were small we did not have enough power to reveal significant differences in terms of infructescence characteristics among *B. gasipaes* varieties as recognized by the Tacana (Table 1). We comment here on tendencies that need corroboration of a larger sample size. For example, infructescences of the red fruit

Table 1. Morphological characteristics and sites of *Bactris gasipaes* infructescences per variety as defined by fruit color (yellow, red, orange). Infructescence length, weight, number of rachillae and number of fruits per infructescence for each sample are indicated.

Samples	Site	Color	Length (cm)	Weight (kg)	Rachillae #	Fruit #
1	Infierno	Yellow	77	3.0	36	110
2	Infierno	Yellow	63	6.3	32	261
3	Infierno	Yellow	54	1.69	37	102
4	Mamuque	Red	56	1.85	35	110
5	Mamuque	Red	53	0.90	38	90
6	Mamuque	Red	53	1.86	35	107
7	San Lorenzo	Orange	61	2.05	39	81
8	San Lorenzo	Orange	60	2.04	38	87
Average			59.6	2.5	36.3	118.5



4. Fruit morphological features for three *Bactris gasipaes* varieties as recognized by the Tacana. **A**. Fruit length; **B**. Fruit weight; **C**. Fruit diameter. Numbers inside the boxplots are means, and different letters above each boxplot indicate statistical differences (p<0.05) among varieties through multiple pairwise comparisons of means. N=number of fruits sampled per variety.

variety tend to be shorter and lighter. The orange fruit variety tends to have a higher number of rachillae, and a lower number of fruits per infructescence than the other two varieties. We found that the yellow variety produced a greater number of fruit per infructescence (102–261), followed by the red (90–110) and orange varieties (81–87) (Table 1). In terms of fruit color, Reyes et al. (1997) found that yellow and red were the predominant cultivated varieties of *B. gasipaes* in Colombia. During our fieldwork, we also observed that yellow and red were the predominant varieties.

A comparison of fruit diameter, length and weight among the three *B. gasipaes* varieties is shown in Figure 4. We found significant differences in all three variables among the different colors ($F_{31,2}$=3.74, P=0.03 for diameter, $F_{31,2}$=50.9, P<0.0001 for length, and $F_{55,2}$=70,0, P<0.0001 for weight). Notably, fruits of the red variety were lighter and smaller. Saldias (1991) conducted a study in Santa Cruz, Bolivia, where he found very similar ranges to ours for fruit diameter and length. However, fruit mass was larger (15–33 g) than the ones we reported in this study (Fig. 4B). Mora Urpí et al. (2003) proposed a race classification system for *B. gasipaes* based on fruit weight. They defined the microcarpa (< 20 g), mesocarpa (20–70 g) and macrocarpa (> 70 g) races, where the latter two corresponded to cultivated varieties. Based on this classification system, the Tacana red fruit variety fits the microcarpa race (mean fruit mass=15.1 g), while both the yellow (mean= 20.1g) and orange (mean=22.1 g) varieties correspond to the mesocarpa race (Fig. 4). The Tacana red fruit variety has small fruits with very fibrous, oily mesocarps and large seeds, and corresponds to *B. gasipaes* var. c*hichagui;* whereas the yellow and orange varieties have starchy mesocarps and are classified as *B. gasipaes* var. g*asipaes* (Fig. 5).

The fruit yield per infructescence was higher for the yellow variety (1.06 kg) than the red (0.44 kg) and orange (0.92 kg) varieties (Table 2). In contrast, potential fruit yield per hectare was higher for the red variety (210 kg/1,000 m^2) than for the yellow (150 kg/1,000 m^2) and orange (110 kg/1,000 m^2) varieties, because the red variety showed a higher number of infructescences per individual (Table 2). The Tacana prefer to extract yellow fruit not because of their higher yield per infructescence, but because of their more palatable flavor and easier access in the forest. This correspondence between higher yield per

5. Mesocarp differences of *Bactris gasipaes* varieties. The red variety (left) has a thin, oily and fibrous mesocarp with large seeds. The yellow variety (right) has a starchy mesocarp with smaller seeds. Photo by Viviana Vargas.

infructescence and preferred flavor might be an indication that fruit flavor might have been selected during the early domestication process in Bolivia. Red fruits were produced in higher quantities per hectare, but these individuals are of difficult access because they grow in fallows. The Tacana do not practice a sustainable fruit harvest because they extract all infructescences from a palm. Since fruit consumption and seed predation by birds and rodents are high in this area, they claim that if they leave some infructescences on the palm, seeds will be predated and regeneration will not be guaranteed. Based on the results we report here and in Moraes et al. (2014) and Vargas (2014), Moraes et al. (2016b) proposed some harvest practices aimed at achieving a good management strategy for *B. gasipaes* in Tumupasa. The recommendations included harvesting no more than 70% of the infructescences per palm, and leaving at least four reproductive adults per hectare. This harvest practice is achievable especially because this is a multistemmed palm with three to four stems per individual (Moraes et al. 2014).

Conclusions

According to the Tacana community, fruit color defines three varieties of *B. gasipaes* in Tumupasa, Bolivia. Varieties with yellow and red fruit were common and easier to find than the orange fruit variety. Fruit yield per infructescence was higher for the yellow variety, but fruit yield per hectare was higher for the red variety, which has smaller and lighter fruit than the other two. The red variety corresponds to the microcarpa race or *Bactris gasipaes* var. *chichagui*, while the yellow and orange varieties belong to the mesocarpa race or *B. gasipaes* var. *gasipaes*.

Literature Cited

BALSLEV, H., N. PANIAGUA, M. MORAES R., M. MACIA, A. PARADA, Y. INTURIAS, Z. PEREZ, J. TERAN, M. ALIAGA, C. GRANDEZ AND A. SERRALTA. 2012. Palmeras de los Leco y sus Usos. Herbario Nacional de Bolivia, Universidad Mayor de San Andrés, Team Graphics srl., La Paz. 45 p.

BATISTA, J. AND C. CLEMENT. 2005. Wild pejibaye (*Bactris gasipaes* Kunth var. *chichagui*) in Southeastern Amazonia. Acta Botanica Brasilica 19: 281–284.

BERNAL, R. AND G. GALEANO. 2013. Cosechar sin Destruir Aprovechamiento Sostenible de Palmas Colombianas. Universidad Nacional de Colombia, Instituto de Ciencias Naturales, Bogotá. 244 p.

CÁMARA-LERET, R., N. PANIAGUA-ZAMBRANA, H. BALSLEV AND M.J. MACÍA. 2014. Ethnobotanical knowledge is vastly underdocumented in northwestern South America. PloS One 9(1): e85794. doi:10.1371/journal.pone.0085794

CIPTA (Consejo Indígena del Pueblo Tacana) & WCS (Sociedad para la Conservación de Vida Silvestre). 2005. Estrategia de Desarrollo Sostenible de la TCO-Tacana con Base en el Manejo de los Recursos Naturales. USAID Bolivia, La Paz. 308 p.

CLEMENT, C.R. 1986. Descriptores Mínimos para el Pejibaye (*Bactris gasipaes* H.B.K.) y sus Implicaciones Filogenéticas. M.Sc. Thesis, Escuela de Biología, Universidad de Costa Rica, San José. 216 p.

CLEMENT, C.R., J. AGUILAR AND D. ARKCOLL. 1998. Composição química do mesocarpo e do óleo de três populações de pupunha (*Bactris*

Table 2. Potential fruit yield per variety of *Bactris gasipaes*.

Variety	Yield in kg/infructescence	Yield in kg/1.000 m2	# infructescences/ palm
Yellow	1.06	150.1	8
Red	0.44	210.9	14
Orange	0.92	110.5	5

gasipaes) do Rio Solimões, Amazonas, Brasil. Revista Brasileira de Fruticultura 20: 115–118.

Clement, C.R. 2006. The Origin of Domesticated Pejibaye (*Bactris gasipaes* var. *gasipaes*). Instituto Nacional de Pesquisas da Amazonia (INPA), Manaus. 16 p.

Díez Astete, A. 2011. Compendio de Etnias Indígenas y Ecoregiones: Amazónica, Oriente y Chaco. Centro de Servicios Agropecuarios y Socio-Comunitarios (CESA), Plural editores, La Paz. 618 p.

Girón, J.M. and L.E. Ordonez. 2016. Determination of carotenoid pigments in palm pear fruit (*Bactris gasipaes*) waste flour. Producción + Limpia 11: 85–93.

Goulding, M. and N. Smith. 2007. Palmeras: Centinelas para la Conservación de la Amazonía. ACCA (Asociación para la Conservación de la Cuenta Amazónica), Lima. 365 p.

Henderson, A. 2000. *Bactris* (Palmae). Flora Neotropica Monograph 79:1–328.

Hissink, K. and A. Hahn. 2000. Los Tacana: Datos sobre la Historia de su Civilización. Tomo II. APCOB (Apoyo Para el Campesino-indígena del Oriente Boliviano), La Paz. 325 p.

Isaza, C., L.A. Nunez, G. Galeano, R. Bernal, A. Nacimiento, R. Dasilva and A. Pineros. 2013. Cartilla para la Cosecha y el Manejo de Palmas Productoras de Frutos (Asaí, Canangucho y Milpesos). Grupo de Investigación en Palmas Silvestres Neotropicales, Instituto de Ciencias Naturales, Universidad Nacional de Colombia, Bogotá.

Lozada G., S. and M. Moraes R. 2013. Estructura poblacional de totaí (*Acrocomia aculeata*, Arecaceae) según presencia de ganado en localidades de Beni y Santa Cruz. Ecología en Bolivia 48: 72–86.

Macía, M.J., P.J. Armesilla, R. Cámara-Leret, N. Paniagua-Zambrana, S. Villalba, H. Balslev and M. Pardo-De-Santayana. 2011. Palm uses in northwestern South America: a quantitative review. Botanical Review 77: 462–570.

Manfío, C., S. Motoiko, C. Magalhaes Dos Santos, L. Pimentel, V. Queiros and A. Sato. 2011. Repetibilidade em características biométricas do fruto de macaúba. Ciência Rural 41: 70–76.

Montúfar, H. and J. Rosas. 2013. Chontaduro/Chontilla. Pp. 77-89, in Valencia, R., R. Montúfar, H. Navarrete and H. Balslev (eds.). Palmas Ecuatorianas. Biología y Uso Sostenible. Primera edición. Herbario QCA de la Pontificia Universidad Católica del Ecuador, Quito.

Mora-Urpi, J., J. Weberand and C. Clement. 1997. Peach palm *Bactris gasipaes* Kunth. Taxonomy, Nomenclature and Geographical Distribution. International Plant Genetic Resources Institute, Rome. 81 p.

Moraes R., M. 2004a. Flora de Palmeras de Bolivia. Herbario Nacional de Bolivia, Instituto de Ecología, Carrera de Biología, Universidad Mayor de San Andrés, La Paz. 262 p.

Moraes R., M. 2004b. Evaluación de palmeras nativas de Bolivia en relación a sus categorías de utilización. Revista Boliviana de Educación Superior en Ciencias - FCPN 3: 63–70.

Moraes R., M. (ed.). 2014a. Palmeras Útiles de Bolivia – Las Especies Mayormente Aprovechadas para Diferentes Fines y Aplicaciones. Herbario Nacional de Bolivia, Universidad Mayor de San Andrés, Plural editores, La Paz. 148 p.

Moraes R., M. (ed.). 2014b. Palmeras de Tumupasa en La Paz, Bolivia. Herbario Nacional de Bolivia, Instituto de Ecología, Carrera de Biología, Universidad Mayor de San Andrés, La Paz. 105 p.

Moraes R., M., J. Sarmiento and E. Oviedo. 1995. Richness and uses in a diverse palm site in Bolivia. Biodiversity and Conservation 4: 719–727.

Moraes R., M., S. Miguez G., V. Vargas Escobar, V. Choque T. and A. Sardán B. 2014. Recomendaciones para Manejo de Palmeras de Tumupasa. Herbario Nacional de Bolivia, Universidad Mayor de San Andrés, Team Graphics, La Paz. 26 p.

Moraes R., M., N. Paniagua Zambrana, R. Cámara-Leret, H. Balslev and M.J. Macía. 2015. Palmas útiles de Bolivia, Colombia, Ecuador y Perú. Pp. 87–102, in Balslev, H., M.J. Macía and H. Navarrete (eds.) Cosecha de Palmas en el Noroeste de Suramérica: Bases Científicas para su Manejo y Conservación. Pontificia Universidad Católica del Ecuador, Quito.

Moraes R., M., R. Hurtado U., V. Choque T., S. Miguez G., G. Toledo Villarroel and F.

MONTOYA. 2016a. Palmeras utilizadas en tierras bajas de Bolivia: Casos de estudio. Pp. 373–388, in LASSO, C.A., G. COLONNELLO AND M. MORAES R. (eds.). Morichales, Canangucales y Otros Palmares Inundables de Suramérica. Parte II: Colombia, Venezuela, Brasil, Perú, Bolivia, Paraguay, Uruguay y Argentina. Serie Editorial Recursos Hidrobiológicos y Pesqueros Continentales de Colombia. Instituto de Investigación de los Recursos Biológicos Alexander von Humboldt (IAvH), Bogotá.

MORAES R., M., V. VARGAS E., S. MIGUEZ G., V. CHOQUE T. AND A. SARDÁN B. 2016b. Estructura poblacional de cinco especies de Arecaceae en Tumupasa (La Paz, Bolivia). Revista de la Sociedad Boliviana de Botánica 9: 39–56.

MIRANDA, J., M. MORAES R. AND R. MULLER. 2009. Estructura poblacional, producción de frutos y usos tradicionales de la palmera "majo" (*Oenocarpus bataua* Mart.) en bosque montano (La Paz – Bolivia). Revista Grupo de Apoyo a la Biología 4: 1–10.

NAVARRO, G. AND M. MALDONADO. 2002. Geografía Ecológica de Bolivia: Vegetación y Ambientes Acuáticos. Centro de Ecología Simón 1 Patiño, Cochabamba. 719 p.

PANIAGUA ZAMBRANA, N.Y., A. BYG, J.C. SVENNING, M. MORAES R., C. GRANDEZ AND H. BALSLEV. 2007. Diversity of palm uses in the western Amazon. Biodiversity and Conservation 16: 2771–2787.

PANIAGUA-ZAMBRANA, N., R. CÁMARA-LERET AND M.J. MACÍA. 2015. Patterns of medicinal use of palms across northwestern South America. Botanical Review 81: 317–415.

PASQUEL, A. AND A. DEL CASTILLO. 2002. Extracción del aceite de la cáscara de *Bactris gasipaes* HBK usando dióxido de carbono presurizado. Revista Amazónica de Investigación Alimentaria 14: 1–14.

RIVAS, M. AND A. BARILANI. 2004. Densidad, potencial productivo y reproductivo de los palmares de *Butia capitata* (Mart.) Becc. de Uruguay. Agrociencia 8: 11–20.

REYES, R., S. BASTIAS, AND E. PENA. 1997. Caracterización de frutos de Chontaduro (*Bactris gasipaes* K.) de la región de Tumaco, Colombia. Revista de Ciencias Agrícolas 1: 45–61.

SALDIAS P., M. 1991. La chonta de Castilla (*Bactris gasipaes* H.B.K.). Taxonomía y algunos datos económicos en Santa Cruz y su distribución en Bolivia. Pp. 115–126, in IV Congreso Internacional sobre la Biología, Agronomía e Industrialización del Pijuayo, Editorial de Universidad de Costa Rica, San José. 368 p.

UGLADE, H. AND L. PINEDA. 2004. Efecto de la sustitución de la harina de trigo con la harina de Pejibaye. Reviteca 10: 1–6.

VARGAS E., V. 2014. Estructura Poblacional, Potencial Productivo de Frutos de la Chima (*Bactris gasiapes*, Arecaeae) en el Area de Influencia de Tumupasa (La Paz, Bolivia). Graduate degree in biology, Universidad Mayor de San Andrés, La Paz. 57 p.

VELARDE, M. AND M. MORAES R. 2008. Densidad de individuos adultos y producción de frutos del asaí (*Euterpe precatoria*, Arecaceae) en Riberalta, Bolivia. Ecología en Bolivia 43: 99–110.

Variation in the Carbon Fraction of Seven Neotropical Palm Species of Different Forest Strata

MILENA CAMBRONERO
Escuela de Biología,
Universidad de Costa Rica,
11501-2060 San Pedro,
San José, Costa Rica
milemd4@yahoo.com

GERARDO AVALOS
Escuela de Biología,
Universidad de Costa Rica,
11501-2060 San Pedro,
San José, Costa Rica and
The School for Field Studies,
Center for Sustainable
Development Studies,
10 Federal St.,
Salem, MA 01970 USA
gerardo.avalos@ucr.ac.cr

AND

CAROLINA ALVAREZ-VERGNANI
Escuela de Biología,
Universidad de Costa Rica,
11501-2060 San Pedro,
San José, Costa Rica
caroav@gmail.com

Palms are highly abundant in tropical forests, representing one of the most relevant groups of angiosperms in various ecological roles and with numerous cultural and economic uses. However, most carbon inventories have focused on dicotyledonous trees and have consistently neglected palms. We describe patterns of carbon fraction in 86 palms of 7 species and different forest strata in the Caribbean lowlands of Costa Rica and measured differences among species, tissues (leaves, stem, roots) and canopy position (understory, subcanopy, canopy). The average carbon fraction was 43.9% ± 1.28, with significant differences among species. Carbon fraction was not related to canopy position but differed between roots, stems and leaves within species. Our results will help to improve estimates of carbon stocks and expand our understanding of how different species and life forms make up the total carbon content of tropical forests.

Palms represent a characteristic component of tropical forests, where they influence forest structure and species diversity (Lieberman et al. 1996, ter Steege et al. 2013). Palms can colonize a wide range of habitats, from the forest understory to the canopy, and from lowland rainforests to the tree line, including wetlands and mangroves (Dransfield et al. 2008, Chomicki et al. 2014, Tomlinson 2016). Several palm species dominate tropical ecosystems such as the *aguajales* of the Peruvian Amazon (*Mauritia flexuosa*, Sampaio et al. 2008) and the *yolillales* of the Osa Peninsula, Costa Rica (*Raphia taedigera*, Grayum 2003). In general, the distribution of palms demonstrates the importance of environmental gradients affecting the abundance and diversity of tropical species (Clark et al. 1996, Svenning 2001, Costa et al. 2009). Palms represent one of the most important groups of angiosperms in terms of cultural and economic uses (Campos & Ehringhaus 2003, Dransfield et al. 2008) and have a crucial role in food webs by providing resources for birds, mammals and insect pollinators (Silberbauer-Gottsberger 1990, Beck 2006).

Despite their evident economic and ecological importance, carbon content studies have not considered palms and have focused instead on dicotyledonous trees, specifically the most abundant and commercially important species (Chave et al. 2001, DeWalt & Chave 2004, Chave et al. 2005, Lorenz & Lal 2010). Aside from Goodman et al. (2013), the few analyses of carbon content in Arecaceae are limited to commercially important species, such as *Bactris gasipaes* (Ares et al. 2002) and *Elaeis guineensis* (Thenkabail et al. 2004, Syahrinudin 2005, Leblanc et al. 2006, Ekadinata et al. 2010, Khasanah et al. 2012, Pulhin et al. 2014). The general assumption is that the percentage of carbon in plant dry biomass, also known as the "carbon fraction," corresponds to 50% (Chave et al. 2008). However, tropical forest species vary in carbon fraction between 41.9–51.6% (Thomas & Martin 2012). Carbon fraction in palms should be within this range, following the data on *Mauritia flexuosa* and *M. aculeata* (51.2%, 48.1% and 48.8% for leaves, stems and roots, respectively; Goodman et al. 2013), and *E. guineensis* (48% for leaves and 52% for stems, Leblanc et al. 2006; 47.5% for leaves, Pulhin et al. 2014; 41.3% per plant). However, since plants distribute carbon according to their life history strategies and their adjustment to local environmental gradients, we should expect palms to adjust their carbon fraction following differences among species and position in the forest profile. The argument driving this expectation is that palms are sensitive to fine environmental gradients and have been indicators of environmental differences at the local scale (Svenning 2001). Canopy position influences light conditions and soil properties, and could act as an environmental filter affecting palm structure and carbon fraction (Kraft et al. 2015). Nevertheless, data on carbon fraction in palms remain very limited (Goodman et al. 2013), which affects the estimation of carbon stocks in rainforests and ignores the contributions of different life forms to the carbon economy (Clark 2007).

The main objective of this study is to describe patterns of variation in carbon fraction in seven palm species of different forest strata, and determine differences according to species, organs (leaves, stems and roots) and canopy position (understory, subcanopy and canopy). We expected overall carbon fraction to be higher in canopy palms since they require higher mechanical support to reach the forest canopy. We also expected understory palms to store more carbon in roots since the light-

Table 1. Palm species from the Caribbean lowlands of Costa Rica analyzed in this study.

Species	Distribution (elev. masl)	Height (m)	Stratum	Tribe
Socratea exorrhiza	S Nicaragua–Brazil (0–750)	25–30	Canopy	Iriarteeae
Iriartea deltoidea	SE Nicaragua–Brazil (0–800)	25–30	Canopy	Iriarteeae
Euterpe precatoria	Belize–Bolivia (0–1150)	26	Subcanopy	Areceae
Prestoea decurrens	Nicaragua–Ecuador (0–900)	10	Understory	Areceae
Chamaedorea tepejilote	Mexico–Colombia (0–1600)	5	Understory	Chamaedoreeae
Geonoma interrupta	S Mexico–Peru (0–850)	6–10	Understory	Geonomateae
Asterogyne martiana	Belize–Ecuador (0–1000)	2	Understory	Geonomateae

limited conditions of the understory makes it more advantageous to store carbon and then use it to grow in pulses as resources become available sporadically depending on sudden changes in canopy structure (Henderson 2002, Sylvester & Avalos 2013). Since selective pressures induced by different light gradients follow canopy position, we expected palms of different forest strata to differ in carbon fraction. Our results will help to refine methodologies estimating and quantifying carbon stocks, as well as to contribute to the available data repository to determine how different species and life forms make up the total carbon accumulated in tropical rainforests (Dewar 1991, Dewar & Cannel 1992, Brown et al. 1996, Achard et al. 2004).

Materials and methods

Study site: We conducted this research in Sarapiquí, Heredia, in the Caribbean lowlands of Costa Rica. Individual palms of different heights were harvested from La Selva Biological Station (10°26′N, 83°59′W, 30–150 m asl, annual precipitation 4162 mm, average daily temperature 25°C), Tirimbina Biological Reserve (10°24′N, 84°06W, 180–220 m asl, annual precipitation 3833 mm, average daily temperature 25.3°C) and the forest of El Progreso agroecological farm (10°30′35′′N, 83°44′39′′W, 45 m asl, annual precipitation of 4000–5000 mm). All three sites present a weak climatic seasonality, with November, December and February being the rainiest months (McDade et al. 1994).

Natural history: The selected species belong to different forest strata and represent diverse palm regeneration strategies and life histories (Table 1). *Socratea exorrhiza* and *Iriartea deltoidea* are canopy palms with prominent stilt roots. In *I. deltoidea* the stilt roots are clustered at the base of the stem, have conspicuous lenticels, and can grow 1.5 m above the ground, whereas in *S. exorrhiza* the stilt roots are well-separated, can grow up to 4 m, and are covered by spines (Henderson et al. 1995). Both species have edible palm hearts, their stems are used for construction and leaves are used for thatching (Sylvester et al. 2012). The species *Euterpe precatoria* is divided into two varieties by Henderson (1995), var. *longevaginata* (stems solitary or cespitose, low and high elevations in the Andes and Central America) and var. *precatoria* (stems solitary, low elevations in the Amazon). In Costa Rica, *E. precatoria* var. *longevaginata* corresponds to a single-stemmed palm, which develops a stilt root cone that in extreme cases may reach over 2 m in height (Avalos & Schneider 2011). *Euterpe precatoria* is a cryptic pioneer species (Kitajima & Poorter 2008) since it regenerates under moderately disturbed conditions, benefiting from increased light levels (Avalos et al. 2013, Avalos 2016), but survives under moderate shade until reaching the subcanopy (Avalos et al. 2013).

Understory species surveyed in this study include *Prestoea decurrens*, *Chamaedorea tepejilote*, *Geonoma interrupta* and *Asterogyne martiana*. *Prestoea decurrens* is a clonal, shade tolerant species with 3–8 stems per genet. *Chamaedorea tepejilote* is a dioecious and single stemmed species, easily identified due to a yellow stripe running along the abaxial side of petioles and foliar rachis (Grayum 2003, Castillo-Mont et al. 1994). *Geonoma interrupta* is a solitary palm reaching 6 m in height (and over 10 m in extreme cases), being considered as one of the tallest species in the genus (Grayum 2003). Finally, *A. martiana* is an understory species with a decumbent stem often reaching 2 m in height, and with simple, bifid leaves. This species is particularly abundant in the Caribbean lowlands (Grayum, 2003).

Field methods: From September 2013 to May 2015, we collected 86 palms (Table 1), taking care to include the full range of sizes observed in the field (from seedlings to adults). We measured stem diameter at 1.3 m above the ground (corresponding to the diameter at breast height, DBH), at half the stem length in palms less than 1.3 m, or immediately above the stilt roots if the height of the stilt root cone was ≥ 1.3 m. We harvested the palms separating stems, roots, and leaves and used a Pesola® Macro-Line Spring Scale (30 ± 0.25 kg) to determine the total fresh biomass of each tissue as well as of the whole palm in the field by adding the weight of the different tissues (stem, roots, leaves). Roots were dug out carefully, collecting all the root material, including fine roots (5 mm in diameter). In cases where it was difficult to extract the totality of the roots, due to their size or depth, a representative section was extracted, and from this, we estimated the total root biomass. We washed the roots in the field and sun dried them for later weighing. To determine the carbon fraction (dry mass of carbon over the total dry mass) we followed Williamson and Wiemann (2010). From each individual palm, we collected 300 mg samples of leaves (including one young, one intermediate and one mature leaf, determined according to their position in the apical meristem), stems (base of the stem, middle part and upper part of the base of the leaf crown) and roots (samples from three different roots). These samples were dried in an oven at 65°C until constant weight (approximately 2 days). Once dried, we ground the samples and determined the carbon fraction in leaves, stems and roots using an automatic analyzer TruSpec CN, LECO Corporation, at the Laboratory of Systematics and Botany of the University of Ulm, Germany, and an automatic elemental carbon and nitrogen analyzer, VarioMacrocube, at the University of Costa Rica. We calculated carbon fraction by palm as the average of carbon fraction of leaves, stem, and roots of each individual plant.

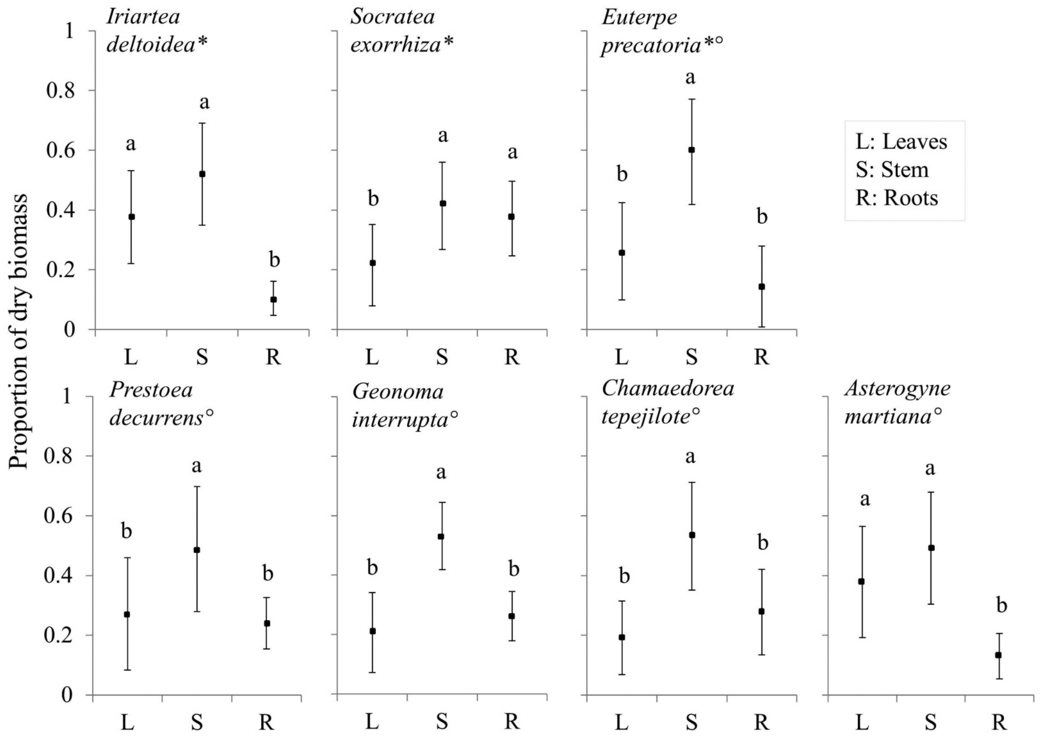
Data analysis: We calculated dry mass fraction by palm as the proportion of dry biomass per unit fresh biomass (dry biomass/fresh biomass). Proportion of dry biomass by tissue, was calculated by dividing the dry biomass by tissue over the total dry biomass. To measure differences in proportion of dry biomass by tissue, and of carbon fraction per species and tissue (leaves, stems and roots), we performed analysis of variance (ANOVA) and a posteriori Tukey-Kramer tests. Before running the ANOVA, species and tissue data (in *A. martiana*, *C. tepejilote* and *G. interrupta*) were transformed following the Box-Cox procedure (Quinn & Keough, 2002) to accommodate for normality and equality of variances. Since *C. tepejilote* is a dioecious species, we performed a covariance analysis to measure differences in diameter and height relationships, and carbon fraction between pistilate and staminate plants. We used JMP10 for all statistical analyses.

Results

We harvested 86 palms ranging in stem length from 0.04 m in an *A. martiana* seedling to 14.8 m in an adult *S. exorrhiza* (Table 2). The average dry mass fraction was 0.31 (± 0.04) and differed between species (Table 2, $F_{6,83}$= 5.15, R^2= 0.27, p= 0.0002). The highest dry mass fraction was observed in *P. decurrens* and the lowest in *I. deltoidea* (Table 2). Proportion of dry biomass by tissue differed in all the species, all of them showing a higher proportion of dry biomass in the stem (Fig. 1). Only in *S. exorrhiza* the proportion of dry biomass in roots was higher than in leaves, and only in *I. deltoidea* and *A. martiana* the proportion of dry biomass in leaves was higher than that of roots (Fig. 1).

Table 2. Range in diameter at breast height (DBH), total height, fresh biomass, dry biomass and mean dry mass fraction (± standard deviation) (levels not connected by the same letter in the case of dry mass fraction are significantly different; Tukey-Kramer test, q= 3.02, α= 0.05) of 7 neotropical palm species of different size from the Caribbean lowlands of Costa Rica.

Species	N	DBH (cm)	Height (m)	Fresh biomass (kg)	Dry biomass (kg)	Dry mass fraction
Socratea exorrhiza	10	2.4–20.6	1.4–14.8	0.7–362.3	0.3–146.4	0.31 ± 0.06^{abc}
Iriartea deltoidea	10	4.4–23.6	1.0–11.2	2.3–344.0	0.6–80.1	0.24 ± 0.04^{c}
Euterpe precatoria	10	3.5–12.8	2.2–12.6	3.5–179.5	1.1–68.9	0.32 ± 0.07^{abc}
Prestoea decurrens	10	5.0–8.6	1.1–11.5	5.3–117.4	2.0–59.6	0.40 ± 0.12^{a}
Chamaedorea tepejilote	22	1.4–3.8	0.36–6.8	0.15–9.6	0.05–4.3	0.28 ± 0.08^{bc}
Geonoma interrupta	9	4.3–9.0	0.7–11.6	1.8–110.4	0.4–54.5	0.34 ± 0.09^{ab}
Asterogyne martiana	15	1.4–3.3	0.04–0.8	0.06–1.82	0.02–0.63	0.32 ± 0.03^{abc}



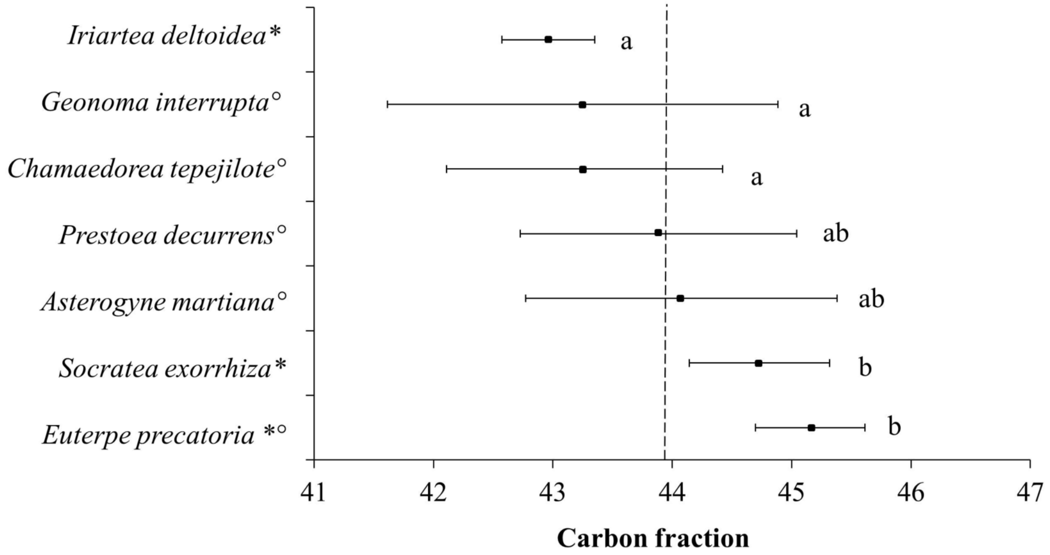
1. Proportion of dry biomass (± 1 S.D.) by tissue in 7 neotropical palm species. Levels not connected by the same letter are significantly different (Tukey-Kramer test, $\alpha = 0.05$, *I. deltoidea, S. exorrhiza, E. precatoria, G. interrupta*: q= 2.48; *P. decurrens*: q= 2.50; *C. tepejilote*: q = 2.39; *A. martiana*: q= 2.43). *Canopy species, *°Subcanopy species, ° Understory species. Sample size follows Table 2.

The lowest carbon fraction was observed in *C. tepejilote*, *G. interrupta* and *I. deltoidea*, and the highest in *E. precatoria* and *S. exorrhiza* (Fig 2). The average carbon fraction across species was 43.9% ± 1.28% (Fig 2). Carbon fraction varied according to species (Fig 2, $F_{6, 79}$= 6.47, R^2= 0.32, p<0.0001) but not between canopy position (canopy, subcanopy, understory). There were differences neither in the diameter vs. height relationships between pistillate and staminate palms in *C. tepejilote* (covariance analysis, $F_{2, 13}$= 0.73, R^2= 0.10, p= 0.50) nor in carbon fraction (ANOVA, $F_{1, 10}$= 0.10, R^2=0.10, p= 0.75). Therefore, we included the 22 *C. tepejilote* palms in subsequent analysis without separating by sex.

Carbon fraction by tissue differed within species, except for *G. interrupta* (Fig 3). Contrary to what we expected, canopy species did not present a higher carbon fraction in the stem; *I. deltoidea* had a higher carbon fraction in roots, whereas in *S. exorrhiza* it was higher in leaves and roots. Carbon content of the subcanopy species *E. precatoria* was higher in leaves, and lower in the stem. Of the understory species, only *P. decurrens* had a higher carbon fraction in roots, whereas in *C. tepejilote* and *A. martiana* it was higher in leaves (Fig 3).

Discussion

The dry mass fraction reported here is comparable to the values obtained by Goodman et al. (2013) for nine palm species in the Amazon. However, Goodman et al. (2013) showed values for roots, stems and leaves (mean 0.35, 0.37 and 0.43, respectively), including samples of the three tissues, only for *Mauritia flexuosa* and *M. aculeata*, whereas for the remaining 7 species only the stem dry mass fraction was reported. Also, Goodman et al. (2013) included palms whose sizes represent later ontogenetic stages excluding seedlings and juveniles. It is necessary to collect more data to obtain general patterns for palms as a group, standardize field and analysis methods to obtain comparable results reflecting the diversity of life forms and growth patterns of palms, include root biomass, and sample a range of sizes more representative of population structure (Thomas & Martin 2012). In our case, the mechanical support

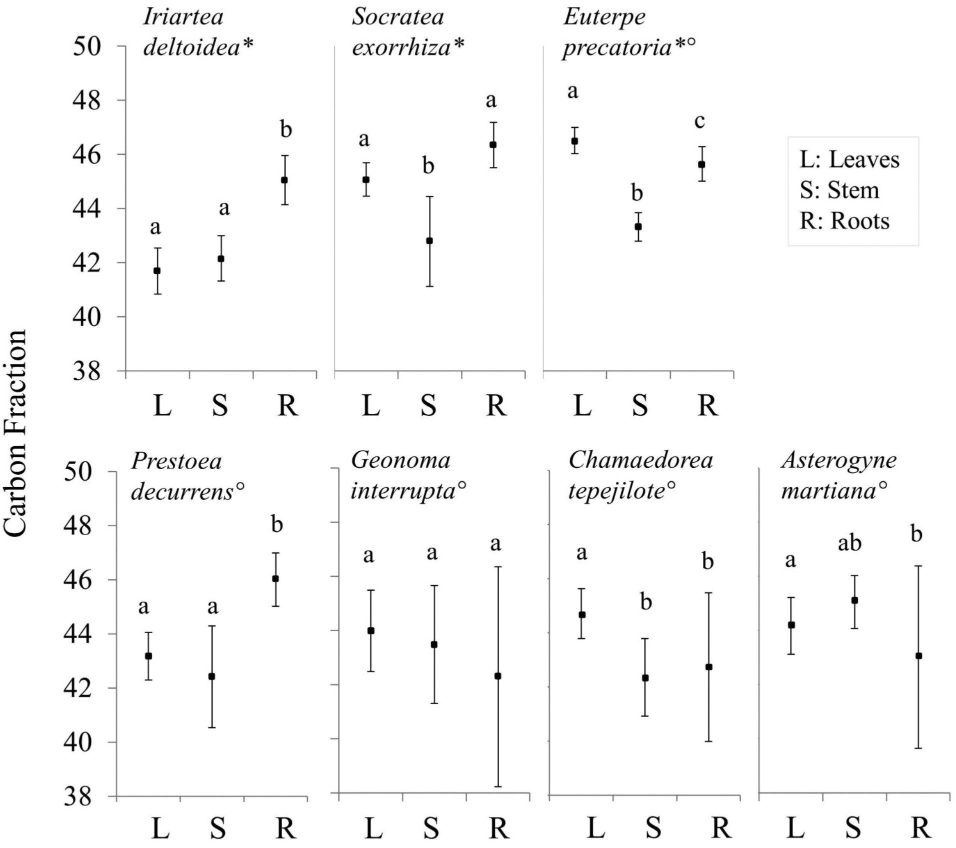


2. Carbon fraction (± 1 S.D.) in 7 neotropical palm species. The dotted line marks the average across species. Levels not connected by the same letter are significantly different (Tukey-Kramer; q = 3.03). *Canopy species, *°Subcanopy species, °Understory species. Sample size as in Table 2.

represented the main compartment for the allocation of dry mass followed by similar magnitudes in leaves and roots but more data is needed to determine if these patterns can be extended to palms in general.

The carbon fraction reported here across palm species was lower than the values resulting from the application of conversion factors recommended for dicotyledonous trees and plant biomass in general (47%–50%) (Thomas & Martin 2012, Chave et al. 2014). Similar to biomass partitioning estimates, uncertainties in the accuracy of allometric models, variation in data processing methods, the lack of estimation of below-ground biomass, the lack of quantification of the volatile carbon fraction, the lack of representation of sufficient species- and site-specific carbon fractions, all combine to influence the estimation of carbon stocks (Thomas & Martin 2012). In addition, the anatomical, developmental and internal tissue properties of palms (which do not possess a vascular cambium) are fundamentally different from that of dicotyledonous trees, and are partially responsible for these differences and justify the need for more group-specific carbon fractions. Palms are built like cantilever beams and thus, the density of stem tissues increases towards the stem base and periphery, and decreases towards the center and top of the stem, which provides sufficient stability without investing more carbon in mechanical support (Rich 1986, Tomlinson 1990, Goodman et al. 2013). Tissue density may not be a good proxy to estimate carbon fraction in palms since it varies with height along the stem (Cambronero 2015). Although conversion factors determined for dicotyledonous trees and plant biomass in general are applied to other plant groups when no data are available, they may introduce large errors in the estimation of carbon stocks in tropical forests (Martin & Thomas 2011) especially in sites where palms are dominant or abundant.

We have previously observed allometric differences in the palm species examined here relative to canopy position. All palms analyzed here show a linear relationship between stem diameter and height (diameter increases to compensate for height increases), with understory species showing steeper height vs. diameter logarithmic regression slopes than canopy species (Avalos et al. in prep). Subcanopy and understory species are more underbuilt than canopy palms and increase height faster than diameter, since they are less massive and require less biomass to reach maximum heights (Henderson 2002). These allometric differences did not translate into differences in carbon fraction following canopy position. Like Martin and Thomas (2011), we observed significant variation in carbon fraction among species but not a clear-



3. Carbon fraction (± 1 S.D.) by tissue in 7 neotropical palm species. Levels not connected by the same letter are significantly different (Tukey-Kramer test, α = 0.05, *I. deltoidea, S. exorrhiza, E. precatoria, G. interrupta*: q= 2.48; *P. decurrens*: q= 2.49; *C. tepejilote*: q = 2.40; *A. martiana*: q= 2.43). *Canopy species, *°Subcanopy species, ° Understory species. Sample size follows Table 2.

cut relationship between carbon fraction and ecological and demographic traits (i.e. canopy position and successional strategy).

The particularities of each species regeneration niche influenced carbon fraction independently of the species canopy position. Species like *I. deltoidea* showed less carbon fraction than *E. precatoria* and *S. exorrhiza*. *Iriartea deltoidea* has stem diameters proportionally larger than those of the latter species with thicker stems conferring greater stability (*I. deltoidea* also had the lowest dry mass fraction but allocated more biomass into aerial parts). Additionally, *I. deltoidea*, *S. exorrhiza*, *P. decurrens* and *A. martiana* presented higher carbon fraction in roots. Resources stored in roots facilitate shade tolerance as well as growth in pulses when light conditions improve (Vandermeer et al. 1974, Lugo & Rivera 1987, Henderson 2002, Homeier et al. 2002). *Iriartea deltoidea* and *S. exorrhiza*, despite being canopy palms, could behave like shade tolerant species during the early stages of regeneration. In contrast, *E. precatoria* benefits from moderate forest disturbance and intermediate light levels during the early stages of the life cycle (Poorter 1999). *Euterpe precatoria* and *C. tepejilote* were the species with the highest carbon fraction in leaves, which may be associated to their preference for more open, disturbed and high light conditions during the first regeneration stages (Valladares & Niinemets 2008, Avalos et al. 2013). The final position in the forest profile did not correlate with the particularities in the regeneration strategies, life cycle, growth patterns and physical structure of the palms examined here.

The carbon fraction values observed here were lower than the values reported for *M. flexuosa* and *M. aculeata* (Goodman et al 2013), and *E. guineensis* (Leblanc et al. 2006, Pulhin et al. 2014). *Mauritia* species and *E. guineensis* belong to different palm tribes (Lepidocaryeae and

Cocoseae, respectively) than the species analyzed here, which could lead to differences in allometry and development, and therefore, to different strategies of carbon fraction. In addition, differences in sample size and methods to estimate carbon fraction differ among studies (Kirby & Potvin 2007). Goodman et al. (2013) collected samples from 3 or 4 individuals per species and calculated carbon content by calorimetry, whereas Leblanc et al. (2016) obtained samples from eight palm trees and used a CN automatic analyzer, and Puhlin et al (2014) calculated carbon fraction only for leaves from 6 palms of different ages, which could explain some of the differences. Similar limitations affect the carbon estimation of trees in general (Kirby & Potvin 2007, Thomas & Martin 2012).

In conclusion, more information on the carbon fraction in tropical palms is needed to identify patterns associated with species differences in ecological and demographic factors. This information is essential to complete our understanding of how the diversity of life forms affects carbon stocks in tropical forests, to improve carbon sequestration models and to expand our understanding of palm regeneration and resource distribution strategies.

Acknowledgments

This investigation was supported by a research grant from the International Palm Society to MC, and scholarships from the Organization for Tropical Studies (MC and CAV), University of Costa Rica (MC) and Tirimbina Biological Reserve (CAV). Nutrient analyses were facilitated by Floria Bertsch at the Centro de Investigaciones Agronómicas, University of Costa Rica, and by Steven Jansen at the Department of Systematic Botany and Ecology, University of Ulm. The Alpízar Chaves family of El Progreso facilitated work in their property. The School for Field Studies provided logistic support. Two anonymous reviewers helped to significantly improve the manuscript.

LITERATURE CITED

ACHARD, F., H.D. EVA, P. MAYAUX, H.J. STIBIG AND A. BELWARD. 2004. Improved estimates of net carbon emissions from land cover change in the tropics for the 1990s. Global Biogeochemical Cycles 18: 1–11.

ARES, A., J. BONICHE, J.P. QUESADA, R. YOST, E. MOLINA AND T.J. SMYTH. 2002. Estimación de biomasa por métodos alométricos, nutrimentos y carbono en plantaciones de palmito en Costa Rica. Agronomía Costarricense 26: 19–30.

AVALOS, G. 2016. Growth of the Neotropical palm *Euterpe precatoria* (Arecaceae) under sun and shade conditions in an agroforestry system in Costa Rica. Brenesia 85–86: 1–8.

AVALOS, G. AND A.R. SCHNEIDER. 2011. Quantification of ramet production in the Neotropical palm *Euterpe precatoria* (Arecacea) in Costa Rica. Ecotropica 17: 31–38.

AVALOS, G., M. FERNÁNDEZ OTÁROLA AND J.T. ENGELN. 2013. Successional stage, fragmentation and exposure to extraction influence the population structure of *Euterpe precatoria* (Arecaeae). Revista de Biología Tropical 61: 1415–1424.

BECK, H. 2006. A review of peccary–palm interactions and their ecological ramifications across the Neotropics. Journal of Mammalogy 87: 519–530.

BROWN, S., J. SATHAYE, M. CANNELL AND P.E. KAUPPI. 1996. Mitigation of carbon emissions to the atmosphere by forest management. The Commonwealth Forestry Review 75: 80–91.

CAMBRONERO, M. 2015. Análisis alométrico de la acumulación de carbono en cuatro especies de palmas de diferentes estratos en tierras bajas del Caribe de Costa Rica. M.Sc. thesis, University of Costa Rica. 75p.

CAMPOS, M.T AND C. EHRINGHAUS. 2003. Plant virtues are in the eyes of the beholders: a comparison of known palm uses among indigenous and folk communities of southwestern Amazonia. Economic Botany 57: 324–344.

CASTILLO-MONT, J.J., N.R. GALLARDO AND D.V. JOHNSON. 1994. The pacaya palm (*Chamaedorea tepejilote*, Arecaceae) and its food use in Guatemala. Economic Botany 48: 68–75.

CHAVE, J., B. RIÉRA AND M.A DUBOIS. 2001. Estimation of biomass in a neotropical forest of French Guiana: spatial and temporal variability. Journal of Tropical Ecology 17: 79–96.

CHAVE, J., C. ANDALO, S. BROWN, M.A. CAIRNS, J.Q. CHAMBERS, D. EAMUS, H. FÖLSTER ET AL. 2005. Tree allometry and improved estimation of carbon stocks and balance in tropical forests. Oecologia 145: 87–99.

CHAVE, J., R. CONDIT, H.C. MULLER-LANDAU, S.C. THOMAS, P.S. ASHTON, S. BUNYAVEJCHEWIN, L. LEONARDO ET AL. 2008. Assessing evidence for a pervasive alteration in tropical tree communities. PLoS Biology 6: e45.

CHAVE, J., M. RÉJOU MÉCHAIN, A. BÚRQUEZ, E. CHIDUMAYO, M.S. COLGAN, W.B. DELITTI, A. DUQUE ET AL. 2014. Improved allometric models to estimate the aboveground biomass of tropical trees. Global Change Biology 20: 3177–3190.

CHOMICKI, G., L.P. BIDEL, W.J. BAKER AND C. J. ALLEMAND. 2014. Palm snorkelling: leaf bases as aeration structures in the mangrove palm (*Nypa fruticans*). Botanical Journal of the Linnean Society 174: 257–270.

CLARK, D.B., D.A. CLARK, P.M. RICH, S. WEISS AND S.F. OBERBAUER. 1996. Landscape-scale evaluation of understory light and canopy structure: methods and application in a neotropical lowland rainforest. Canadian Journal of Forest Research 26: 747–757.

CLARK, D.A. 2007. Detecting tropical forests' response to global climatic and atmospheric change: current challenges and a way forward. Biotropica 39: 4–19.

COSTA, F.R., J.L. GUILLAUMET, A.P. LIMA AND O.S. PEREIRA. 2009. Gradients within gradients: The mesoscale distribution patterns of palms in a central Amazonian forest. Journal of Vegetation Science 20: 69-78.

DEWALT, S.J AND J. CHAVE. 2004. Structure and biomass of four lowland Neotropical forests. Biotropica 36: 7–19.

DEWAR, R.C. 1991. Analytical model of carbon storage in the trees, soils and wood products of managed forests. Tree Physiology 8: 239–258.

DEWAR, R.C. AND M.G.R. CANNELL. 1992. Carbon sequestration in the trees, products and soils of forest plantations using UK samples. Tree Physiology 11: 49–71.

DRANSFIELD, J., N.W. UHL, C.B. AMUSSEN, W.J. BAKER, M.M. HARLEY AND C.E. LEWIS. 2008. Genera Palmarum: the Evolution and Classification of Palms. Kew Publishing Royal Botanic Gardens, London.

EKADINATA, A.E., N. KHASANHA, S. RAHAYU, S. BUDIDARSONO AND M. VAN NOORDWIJK. 2010. Carbon Footprint of Indonesian Palm Oil Production: Sample Design and Methodology. World Agroforestry Centre, International Centre for Research in Agroforestry, Indonesia.

GOODMAN, R., O.L. PHILLIPS, D. TORRES, L. FREITAS, S. TAPIA-CORTESE, A. MONTEAGUDO AND T. BAKER. 2013. Amazon palm biomass and allometry. Forest Ecology and Management 310: 994–1004.

GRAYUM, M.H. 2003. Arecaceae. Pp. 201–293, in HAMMEL, B.E., M.H. GRAYUM, C. HERRERA AND N. ZAMORA (eds.). Manual de Plantas de Costa Rica. Vol. III. Missouri Botanical Garden, St. Louis, Missouri.

HENDERSON, A. 1995. The Palms of the Amazon. Oxford University, New York, USA.

HENDERSON, A., G. GALEANO AND R. BERNAL. 1995. Field Guide to the Palms of the Americas. Princeton University Press, New York.

HENDERSON, A. 2002. Evolution and Ecology of Palms. The New York Botanical Garden, New York, USA.

HOMEIER, J., S.W. BRECKLE, H. DALITZ, C. LEVERS AND R. ORTIZ. 2002. Demography, spatial distribution, and growth of three arborescent palm species in a tropical premontane rain forest in Costa Rica. Ecotropica 8: 239–247.

KHASANAH, N., M. VAN NOORDWIJK, A. EKADINATA, S. DEWI, S. RAHAYU, H. NINGSIH, A. SETIANWAN, E. DWIYANTI AND R. OCTAVIANI. 2012. The Carbon Footprint of Indonesian Palm Oil Production. (Technical Brief No 25: Palm oil series). World Agroforestry Centre – ICRAF, SEA Regional Office, Bogor, Indonesia.

KIRBY, K. AND C. POTVIN. 2007. Variation in carbon storage among tree species: implications for the management of a small-scale carbon sink project. Forest Ecology and Management 246: 208–221.

KITAJIMA, K. AND L. POORTER. 2008. Functional basis for resource niche partitioning by tropical trees. Pp. 160–181, in CARSON, W.P. AND S.A. SCHNITZER (eds.). Tropical Forest Community Ecology. Wiley-Blackwell, New Jersey.

KRAFT, N. J., P.B. ADLER, O. GODOY, E.C. JAMES, S. FULLER AND J.M. LEVINE. 2015. Community assembly, coexistence and the environmental filtering metaphor. Functional Ecology 29: 592–599.

LEBLANC, H., R. RUSSO, J.J. CUEVA AND E. SUBÍA. 2006. Fijación de carbono en palma aceitera en la región tropical húmeda de Costa Rica. Tierra Tropical 2: 197–202.

LIEBERMAN, M., D. LIEBERMAN AND D.S. HARTSHORN. 1996. Tropical forest structure and com-position on a large-scale altitudinal gradient in Costa Rica. Journal of Ecology 84: 137–152.

LORENZ, K. AND R. LAL. 2010. Carbon Sequestration in Forest Ecosystems. Springer Verlag, Berlin, Germany.

LUGO, A.E. AND C.T. RIVERA. 1987. Leaf production, growth rate, and age of the palm *Prestoea montana* in the Luquillo Experimental Forest, Puerto Rico. Journal of Tropical Ecology 3: 151–161.

MARTIN, A.R. AND S.C. THOMAS. 2011. A reassessment of carbon content in tropical trees. PloS One 6: e23533.

MCDADE, L.A., K.S. BAWA, H.A. HESPENHEIDE AND G.S. HARTSHORN (eds.) 1994. La Selva: Ecology and Natural History of a Neotropical Rainforest. University Chicago Press, Chicago.

POORTER, L. 1999. Growth responses of 15 rainforest tree species to a light gradient: The relative importance of morphological and physiological traits. Functional Ecology 13: 396–410.

PULHIN, F.B., R.D. LASCO AND J.P. URQUIOLA. 2014. Carbon sequestration potential of oil palm in Bohol, Philippines. Ecosystems & Development Journal 4: 14–19.

QUINN, G.P. AND M.J. KEOUGH. 2002. Experimental Design and Data Analysis for Biologists. Cambridge University Press, Cambridge.

RICH, P. 1986. Mechanical architecture of arborescent rain forest palms. Principes 30: 117–131.

SAMPAIO, M.B., I.B. SCHMIDT AND I.B. FIGUEIREDO. 2008. Harvesting effects and population ecology of the buriti palm (*Mauritia flexuosa* L. f., Arecaceae) in the Jalapão Region, Central Brazil. Economic Botany 62: 171–181.

SILBERBAUER-GOTTSBERGER, I. 1990. Pollination and evolution in palms. Phyton, 30: 213–233.

SVENNING, J.-C. 2001. On the role of microenvironmental heterogeneity in the ecology and diversification of Neotropical rain-forest palms (Arecaceae). Botanical Review 67: 1–53.

SYAHRINUDIN. 2005. The Potential of Oil Palm and Forest Plantations for Carbon Sequestration on Degraded Land in Indonesia. Ecology and Development Series 28, Germany.

SYLVESTER, O., G. AVALOS AND N. CHÁVES FERNÁNDEZ. 2012. Notes on the ethnobotany of Costa Rica's palms. Palms 56: 190–201.

SYLVESTER, O. AND G. AVALOS. 2013. Influence of light conditions on the allometry and growth of the understory palm *Geonoma undata* subsp. *edulis* (Arecaceae) of neotropical cloud forests. American Journal of Botany 100: 2357–2363.

TER STEEGE, H., N.C.A. PITMAN, D. SABATIER, C. BARALOTO, R.P. SALOMAO, J.E. GUEVARA ET AL. 2013. Hyperdominance in the Amazonian tree flora. Science 342: 325–342.

THENKABAIL, P.S., N. STUCKY, B.W. GRISCOM, M.S. ASHTON, J. DIELS, B. VAN DER MEER AND E. ENCLONA. 2004. Biomass estimations and carbon stock calculations in the oil palm plantations of African derived savannas using IKONOS data. International Journal of Remote Sensing 25: 1–27.

THOMAS, S.C. AND A.R. MARTIN. 2012. Carbon content of tree tissues: a synthesis. Forests 3: 332–352.

TOMLINSON, P.B. 1990. The Structural Biology of Palms. Oxford University Press, New York.

TOMLINSON, P.B. 2016. The Botany of Mangroves. Cambridge University Press.

VALLADARES, F. AND Ü. NIINEMETS. 2008. Shade tolerance, a key plant feature of complex nature and consequences. Annual Review of Ecology, Evolution, and Systematics 39: 237–257.

VANDERMEER, J.H., J. STOUT AND G. MILLER. 1974. Growth rates of *Welfia georgii*, *Socratea durissima* and *Iriartea gigantea* under various conditions in a natural rain forest. Principes 18: 148–154.

WILLIAMSON, G.B. AND M.C. WIEMANN. 2010. Measuring wood specific gravity… correctly. American Journal of Botany 97: 519–524.

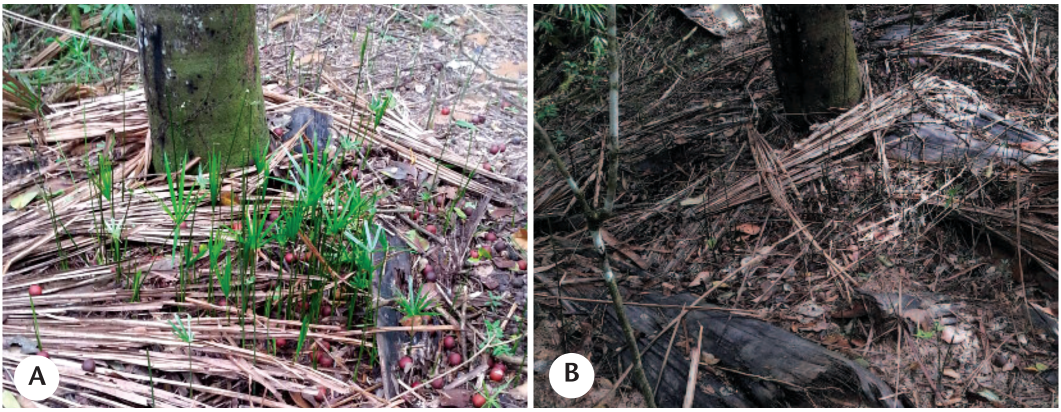
Do Leaf-Cutter Ants Affect *Mauritia flexuosa* Population Structure?

LINTON LEE ARNEAUD
Department of Life Sciences,
The University of the West Indies,
St Augustine, Trinidad & Tobago
lintonarneaud1@gmail.com

Leaf-cutters ants, *Atta cephalotes* (Formicidae), are known to select the leaves of pioneer plant species due to their high nutrient content and low chemical defenses (Farji Brener 2001). The ants do not feed on the leaves directly, but use the leaves as a growing medium to farm an edible fungus (Shripat 2011). Here I report observations of how *A. cephalotes* may be threatening the seedling bank of the palm *Mauritia flexuosa* L.f.

In November 2016, during a walk through the black-water swamp at KP-Quarry in the Aripo Savana Environmentally Sensitive Area (ASESA), Trinidad and Tobago (UTM 20P 696253, 1174711. Datum: WGS84), I noticed that all the leaves of *M. flexuosa* seedlings less than 1 m tall found under a parent palm were completely stripped by leaf-cutter ants. I found a large nest a few meters away, and all palm seedlings as far as the eye could see were missing leaves. What was particularly interesting was that there was little evidence of juveniles within the population.

In April 2017, I made the same observations under the same parent palm: however, this time I recorded some data. Some 201 seedlings were predated by *A. cephalotes* under the parent palm. Another neighboring female palm experienced the same fate, with all the leaves from ca. 100 seedlings being eaten. I established a 10-m radius circular quadrat after walking 20 m northwest from the ant nest. Here, well over 1000 seedlings under 10 female palms were observed to be predated. This pattern remained similar outside the sample quadrat. After a detailed investigation of a



1. *Mauritia flexuosa* seedlings repeatedly being predated by *Atta cephalotes*, Trinidad. **A.** November 2016 and; **B.** April 2017. Photo by Linton L. Arneaud.

10,000 m^2 area, I can say that this entire palm population was under attack by the leaf-cutter ants. I observed that, as adult palms are senescing and dying, they are not being replaced by seedlings and juveniles. This observation begs the question as to whether the population is sustainable when seedlings are repeatedly predated by leaf cutter ants (Fig 1).

I then carried out investigations on the main *M. flexuosa* population within the ASESA (Sav 1, 2, 5 and 6) during April to June 2017. Three smaller ant nests were found, but I found no evidence that the leaf-cutter ants attacked palm seedlings. This lack of predation could be due to several reasons, singly or in combination, such as differences in water level and canopy coverage, availability of preferred food sources or abundance of leaf-cutter ant predators. Further experiments are required to establish what condition(s) favor *A. cephalotes* population growth and food-substrate choices in the swamp. A long-term experiment is warranted to ascertain if leaf-cutter ants negatively affect *M. flexuosa* populations in the ASESA and elsewhere.

LITERATURE CITED

FARJI BRENER, A.G. 2001. Why are leaf cutting ants more common in early secondary forests than in old growth tropical forests? An evaluation of the palatable forage hypothesis. Oikos 92: 169-177.

SHRIPAT, V. 2011. The online guide to the animals of Trinidad and Tobago. https://sta.uwi.edu/fst/lifesciences/documents/Atta_cephalotes.pdf. The University of the West Indies. Accessed October 23, 2017.

Juania australis – a First Flowering in Ireland

BRENDAN SAYERS,
KAREN FOLEY
AND
DAVID FOLEY
National Botanic Gardens
Glasnevin
Dublin D09 VY63
Ireland
corresponding author:
brendan.sayers@opw.ie

Juania australis **has begun to flower in Ireland.**

Juania australis, the Chonta palm, is an island endemic from Robinson Crusoe Island or Más a Tierra of the Juan Fernández Islands off the coast of Chile in the South Pacific Ocean where it grows in montane hardwood and tree-fern forests. It sits alone in its genus, having evolved in isolation some 670 miles from mainland Chile. The species was economically important and sought after for its "attractive stems with black vascular bundles" (Stuessy et al. 1983) and is currently listed as vulnerable (VU) by the International Union for the Conservation of Nature and is protected in its natural habitat. The island was declared a National Park in 1935 and a Biosphere Reserve in 1977. The palm is a subject of a conservation project run by the Corporación Nacional Forestal (National Forest Corporation), a private, non-governmental organisation, funded and overseen by the Ministeria de Agricultura (Ministry of Agriculture of Chile). Its rarity is reflected in the price of its seed. In July 2017, a packet of 10 seeds was available online for €194.40.

In a recent issue of PALMS, Hamann (2017) gave an account of *Juania australis* and stated, "it is glacially slow and notoriously difficult to grow," and indeed, cultivated plants of *Juania australis* are seldom seen. On the Chilean mainland, mature specimens are known from the Vina del Mar Botanic Garden, the city of Concón and the Edwards Estate in the Valpairíso region. Plants are also cultivated on Isla Illeifa, Lago Ranco in the Los Ríos region. Outside Chile the species is considered difficult to cultivate and there are very few known examples of established plants. In North America, semi-mature specimens are known from the San Francisco Botanical Garden, Huntington Botanic Gardens and Lakeside Palmetum. Recent online communications indicate that gardeners are growing it in the UK, Malta, France and Ireland. However, it is the New Zealand and Irish plants that have survived longest and reached maturity. Attempts to obtain an update on plants in New Zealand for this article have been unsuccessful.

Following a visit to the Royal Horticultural Society's garden, Rosemoor, in 1995, David Robinson returned to his garden of Earlscliffe, County Dublin, Ireland and planted a gifted plant of *Juania australis*. This was the first time the species was trialled as an outdoor specimen on the island, and though cautioned about the difficulty of cultivation, David planted it under the conditions afforded every other plant in his garden – "live or let die" (Fig. 1). Plants at Rosemoor died within a few years of planting (pers. comm. C. Bailes via Jonathan Webster).

1. David Robinson with the juvenile *Juania australis* in his garden, Earlscliffe, Bailey, Co. Dublin in 2003.

The Earlscliffe plant thrived in its new home and was undamaged by the severe winters of 2010 and 2011. In June 2017, it produced its first inflorescence and can now be identified as a female (Fig. 2). This specimen at Earlscliffe caused wonder and envy but also encouraged others to attempt to cultivate it (Fig. 3). In Ireland plants now grow at Kells Bay House, Co. Kerry (Fig. 4), a private garden in Greystones, and at the National Botanic Gardens, Kilmacurragh, both in Co. Wicklow. Kells Bay is not only a garden but also a private

2. The female inflorescence on the plant at Earlscliffe in June 2007.

fern and palm nursery, and young plants of *Juania australis* are available for purchase. The proprietor, Billy Alexander, has sold plants to gardeners in Ireland, Britain and France. Plants at Kells Bay were badly affected during the severe winters of 2010 and 2011 but have all recovered. The Greystones specimen was unaffected by the cold weather.

3. The Earlscliffe plant with Karen Foley in 2016.

In 1977, Harold E. Moore identified *Juania australis* as a palm most in need of protection, and in 1978, the International Union for the Conservation of Nature (IUCN) identified the species among five recommended for ex-situ cultivation in its red data book (Lucas & Synge 1978). In 2001 Maunder et al., studying the contribution of ex situ cultivation in botanic gardens towards palm conservation, showed that, of the five IUCN species recommended

4. *Juania australis* in the Ladies Garden, Kells Bay House and Gardens, Co. Kerry.

for ex situ cultivation, *Juania australis* was not recorded as being cultivated in the 35 botanic gardens collections surveyed. Given the difficulties of cultivation and success in bringing plants to maturity outside Chile, it appears certain areas in Ireland may provide suitable sites for ex situ breeding populations.

Acknowledgements

Appropriate appreciations to Paul Maher, Billy Alexander, Jonathan Webster, Donald Hodel and Chris Bailes for assistance with this article and most especially to the memory of a most generous and gentlemanly gardener, David Robinson. We also acknowledge www.earlscliffe.com

LITERATURE CITED

HAMMAN, G. 2017. Exploring Robinson Crusoe or In Search of *Juania australis*. Palms 61: 57–63.

LUCAS G. AND H. SYNGE. 1978. The IUCN Plant Red Data Book. IUCN Switzerland

MAUNDER M., B. LYTE, J. DRANSFIELD AND W.J. BAKER. 2001. The conservation value of botanic garden palm collections. Biological Conservation 98: 259–271.

MOORE, H.E., JR. 1977. Endangerment at the specific and generic levels in plams. pp. 267–282, In: G.T. PRANCE (ed.), Extinction is Forever. The New York Botanical Garden, USA.

STUESSY, T.F, R.W. SANDERS AND O.R. MATTHEI. 1983. *Juania australis* revisited in the Juan Fernández Islands, Chile. Principes 27: 71–74.

Charles Wright and Cuban Palms. 1. Resurrection of *Coccothrinax acuminata*

Celio E. Moya López
Sección de Palmas,
Sociedad Cubana de Botánica
90 South Blvd. Apt. 2C,
Boynton Beach, Florida
33435 USA
Celio.Moya@gmail.com

and

Isidro E. Méndez Santos
Universidad de Camagüey
"Ignacio Agramonte Loynaz"
Carretera de
Circunvalación Norte, Km 5 ½,
Camagüey, Cuba.
isidro.mendez@reduc.edu.cu

A new taxonomic treatment to demonstrate the legitimacy of the name *Coccothrinax acuminata* Becc. (Arecaceae) is presented. Two taxa, *Coccothrinax miraguama* var. *novo-geronensis* and *C. miraguama* subsp. *arenicola*, are treated as new synonyms. Three lectotypes are designated, and 38 isolectotypes not mentioned in previous publications are indicated.

The palm family has undergone an important process of diversification in Cuba, resulting in 15 genera with 79 species, 8 hybrids and 11 infraspecific taxa (Moya & Leyva 2000, updated by the first author). However, recent publications (Suárez 2015, Verdecia 2016, Moya et al. 2017), suggest that the taxonomic richness of the group in Cuba is not yet fully known.

This abundance of palms in Cuba has attracted a great deal of attention. Numerous researchers from various countries have made contributions, but they have not always taken into account the historical record. Therefore, for the development of a robust taxonomy of Cuban palms today, the task of reanalyzing historical information becomes a priority, in order to correct errors and eliminate possible causes of ambiguity and confusion.

In the genus *Coccothrinax*, restricted within the Caribbean Basin, 55 species have been described, seven infraspecific taxa and one hybrid. Cuba is its center of diversity where 39 species are found (38 of them endemic), seven

1. Stem with leaf sheaths and older infrutescence of *Coccothrinax acuminata* in Cortés, Pinar del Río. Photo by C.E. Moya.

2. *Coccothrinax acuminata* growing together with *Acoelorrhaphe wrightii* (left and background) in Cortés. Photo by C.E. Moya.

subspecies and one hybrid. Nine species have been reported in Hispaniola (seven of them endemic). Of the remaining, four are limited to the islands, two share their distribution between the islands and continental territory and only one is confined to the mainland (Jestrow et al. 2017).

The taxonomic treatment of this genus cannot be considered complete. On the one hand, new descriptions continue to be published; three occurred in the last four years (Mejía & García 2013, Suárez 2015 and Moya et al 2017). On the other hand, it is still necessary to refine part of the nomenclature used in previous accounts of currently recognized taxa.

A particularly complex taxonomic and nomenclatural situation occurs in western Cuba, around what could preliminarily be called the "*Coccothrinax acuminata* complex," a name used by different authors, although not always legitimately. It is a group that grows in the southern parts of the provinces of Pinar del Río and Artemisa, as well as in central and northern Isla de la Juventud. Taxa in this complex are characterized by the presence of short, pendulous mature infructescences, with a rachis partially down-curved, leaves that are 5/4 orbicular, with segments 12–15 cm long measured from the "shoulder" to the apex, thin leaf sheath strands 0.5–1 mm wide and densely woven in three layers (Fig. 1). In addition to the main species, two other infraspecific taxa, *Coccothrinax miraguama* (*novo-geronensis*) Becc. and *C. miraguama* subsp. *arenicola* (León) Borhidi & O.Muñiz, are involved.

The objectives of this paper are to offer a new taxonomic system that better reflects the natural variability in this complex, to evaluate the nomenclature used historically for it, to determine the accepted name, to reveal the location of the type material in different herbaria and to order the synonymy.

Materials and Methods

The nomenclature and taxonomy of what we refer to in this paper as "*Coccothrinax acuminata* complex" was investigated. A review was done of the protologues of the names used by different authors and of the different descriptions available in the main treatments. Expedition notes and species catalogs were also studied. A taxonomic study was made from a review of herbarium specimens and field studies conducted by the first author for over 30 years.

The following works were consulted: Sauvalle (1871, 1873), Gómez de la Maza (1893), Sargent (1899), Schumann (1901), Beccari (1907, 1913), Britton (1910, 1916), Shafer (1913), Jennings (1917), León (1918), Dahlgren (1936), León (1939, 1946), Borhidi and Muñiz

(1971), Glassman (1972), Muñiz and Borhidi (1982), Chiappy et al. (1986), Cejas and Herrera (1995), Hernández et al. (1995), Moya and Leiva (2000), Govaerts and Dransfield (2005), Govaerts et al. (2011), Acevedo Rodríguez and Strong (2012), Novo et al. (2015) and Greuter and Rankin (2016). The materials used by Beccari were reviewed in Cuccuini and Nepi (2006). The effectiveness, validity and legitimacy of each name used was checked using the International Code of Nomenclature for algae, fungi, and plants (ICN) (McNeill et al. 2012).

128 specimens of 38 collections (including 45 types) were reviewed from the following herbaria: BRU, CM, F, FI, GH, HAC, HCM, K, LE, M, MO, NY, P, US (acronyms *sensu* Thiers, 2016). Special attention was paid to the study of specimen duplicates (*Wright 3966*) in seven of these herbaria, as well as clarification of the location of the lectotypes and isolectotypes. A study was made of the exact locations of the collections made by Charles Wright that are basic to an understanding of the taxonomy and nomenclature of the taxon, as was a study done of the contrasting data annotated by him on herbarium labels. We also reviewed information available in the literature (Underwood 1905, Howard 1988) and the current cartography and phytogeography of the region (Borhidi 1996).

Field expeditions were carried out in localities where the presence of the taxon was known in the province of Pinar del Río: north of Cortés (Fig. 2), municipality Sandino; near Herradura, municipality Consolación del Sur; savannahs of El Sábalo, municipality Guanes, as well as the area surrounding La Cañada, La Fe, Siguanea, Las Nuevas, Hotel Colony and Nueva Gerona of Isla de la Juventud. Also visited were the localities of Las Pozas, Cajalbana and Viñales in western Cuba, where other species of the genus are reported. Diagnostic characters were studied *in situ*, and a preliminary key was developed to differentiate it from the other *Coccothrinax* species in that part of the country.

Results and Discussion

The evaluation and comparison of morphological, phenological and phytogeographic evidence, from plants *in situ* (during field trips) and from 126 herbarium specimens of *Coccothrinax* collected in western Cuba led the main author to the preliminary conclusion that all specimens previously designated as *C. acuminata*, *C. miraguama* (*novo-geronensis*) and C. *miraguama* subsp. *arenicola* constitute a single taxon.

Taxonomic and nomenclatural history

The first event relevant to the group under study was the collection of *Coccothrinax acuminata* made by Charles Wright and given the number *3966*, from which was established the first of the names involved. The labels of Wright's herbarium refer only to the country but do not specify the exact location in which they were collected (Howard 1988). However, a specimen in the Gray Herbarium, GH28253, has a note written by Wright, which says: "*Balestena Feby 23.*" According to Gray (cited by Underwood 1905 and Howard 1988), Balestena was a cattle farm, property of José Blain, located at the southern base of the mountains opposite Bahía Honda, Pinar del Río. The boundaries of the farm were the Sierra Rangel to the north, Santa Cruz to the south, the river of the same name to the east and the Taco Taco River to the west. This locality is currently within the municipality of San Cristóbal, province Artemisa, and is part of the biogeographical district Sabaloense (Borhidi 1996).

The name *Thrinax acuminata* was initially used by Sauvalle (1871) for the specimen *Wright 3966*, without description, diagnosis or reference to a previous one, which makes it a *nomen nudum*. Subsequently the name continued to be used in Sauvalle (1873), Gómez de la Maza (1893) and Sargent (1899), but none of them fulfilled Article 38 of the Code. Sargent in Schumann (1901) transferred it to *Coccothrinax*, but this combination continued to constitute a *nomen nudum*. Beccari (1907) first used the name *Coccothrinax acuminata* (based on *Coccothrinax acuminata* Sargent 1899) as a valid name, as it was accompanied by a description and a type designation (*Wright 3966*), although he did not indicate the herbarium in which the type was deposited. In 1972, Glassman reconsidered its taxonomic validity and indicated that, in his opinion, the holotype was deposited in A (herbarium of the Arnold Arboretum, Harvard University).

The type material used for the description that validated *Coccothrinax acuminata* also merits careful analysis. The specimen chosen as the lectotype is K000462859 (*http://specimens.kew.org/herbarium/K000462859*) deposited at Kew (Fig. 3), because Beccari used the material for

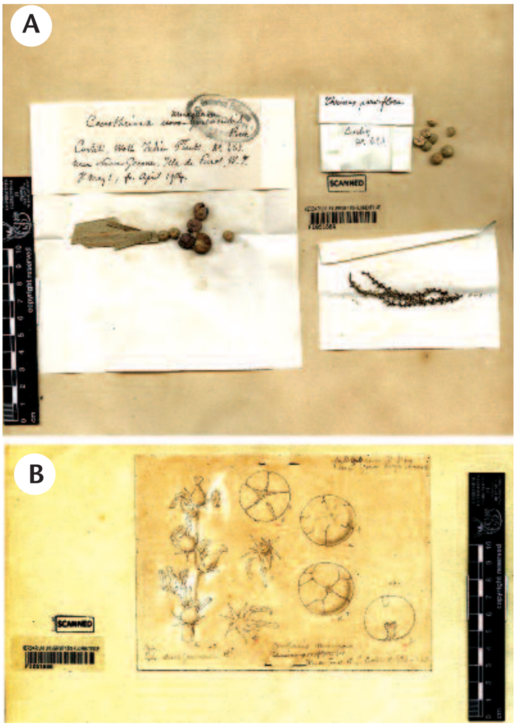
3. Kew specimen of *Wright 3966* with Beccari's handwritten annotation (barcode K 000462859), selected here as lectotype of *Coccothrinax acuminata* Becc. © copyright of the Board of Trustees of the Royal Botanic Gardens, Kew.

his description of the reproductive characters and handwrote an annotation, "*Coccothrinax acuminata* (Sargent) O. Becc III/1907." This same specimen was examined previously by J.D. Hooker, who handwrote on the sheet, "*Thrinax acuminata* Griseb. & Wendl. Cuba 7/[18]71," apparently referring to the *nomen nudum* used by Sauvalle in 1871. This specimen at Kew, with Beccari's handwritten annotation, must be the lectotype of *C. acuminata*. This supersedes all other type designations, such as "isotype of *Coccothrinax acuminata*" on the specimens of *Wright 3966* held at GH (Gray Herbarium of Harvard University). The claim by S.F. Glassman (1972) that the type is a specimen deposited in A is in error; the specimens are present only in GH (GH28253, GH28254 and GH28255) and not in other herbaria of Harvard. Read in 1969 noted as isotypes, with corresponding annotations, duplicates of *Wright 3966* in F, NY and US, while Kellogg annotated those of GH. However, none of them had been indicated as types in any publications. In this article, a total of 19 new isolectotypes are indicated, among which, in addition to those previously mentioned, are those existing in BRU, FI, GH, NY, P and US.

In later years, Beccari (1913), Burret (1929) and Dahlgren (1936) accepted the name *Coccothrinax acuminata*, but León (1939) considered it to be synonymous with *C. miraguama* (Kunth) Becc. var. *miraguama*. Many authors (León 1946, Muñiz & Borhidi 1982, Henderson, Galeano & Bernal 1995, Moya & Leiva 2000, Govaerts & Dransfield, 2005, Govaerts et al. 2011, Acevedo Rodríguez & Strong 2012, Greuter & Rankin, 2016) followed León (1939).

On the other hand, Beccari (1913) used the designation *Coccothrinax miraguano* (*novo-geronensis*), without specifying infraspecific rank, for flower and seed drawings of the specimen *Curtiss 423,* although he did not clarify the herbarium he consulted. It is assumed that the specimen is present in his herbarium at FI (Natural History Museum, Florence, Italy). He accompanied all this with

4. *Coccothrinax miraguama* var. *novo-geronensis* Becc. **A**. *Curtiss 423* with Beccari's handwritten annotation (barcode FI 051884), selected here as lectotype. **B**. Original drawings for Figure 169 in Beccari (1913). © copyright of the Natural History Museum of Florence.



5. Vegetation at Los Indios, Isla de la Juventud, with *Coccothrinax acuminata*. Photo by Michael Calonje.

a diagnosis in which he pointed to the "almost sessile" flowers of this palm from the Isla de Pinos (currently Isla de la Juventud) as the feature differentiating it from *C. miraguano* from mainland Cuba. Beccari (1931) transcribed this name as a variety.

León (1939), although he mentioned Beccari (1913), was unaware of Dahlgren's (1936) designation and indicated *Curtiis 423* as one of the paratypes of *C. miraguama* var. *arenicola* León, described in his work. Glassman (1972) accepted Dahlgren (1936) and indicated the duplicate deposited in US as holotype, a criterion not shared by the authors of this article, as explained later. Henderson, Galeano and Bernal (1995) considered *Coccothrinax miraguama* var. *novo-geronensis* Becc. as a synonym of *Coccothrinax miraguama*, but the taxon has been ignored by all the following authors: Burret (1929), León (1946), Muñiz & Borhidi (1982), Moya and Leiva (2000), Govaerts and Dransfield (2005) and Govaerts et al. (2011), Acevedo Rodríguez and Strong (2012) and Greuter and Rankin (2016).

To designate the lectotype of *Coccothrinax miraguano* var *novo-geronensis*, priority was given to samples deposited in FI, where Beccari carefully studied *Coccothrinax* materials from the West Indies. The specimen *FI 051884* is designated as a lectotype, which Beccari (1913) used for the diagnosis and drawings (Fig. 4). The statement made by Glassman (1972) is rejected, because there is no evidence that the US duplicates were reviewed by Beccari; moreover, to be a holotype, the specimen would have to have cited explicitly by Beccari, which it was not. None of the 17 duplicates of *Curtiss 423*, deposited in CM, FI, HAC, K, LE, M, MO, NY, and US, had been previously mentioned as part of the typological material of *Coccothrinax miraguama* var. *novo-geronensis* Becc.

Finally, *Coccothrinax miraguama* var. *arenicola* was described by León (1939), who quotes in the protologue three specimens from the same locality: *León 16146*, *León 16147* and *León 16148*, without designating a holotype. León himself (1946) named it as a variety, nevertheless Borhidi and Muñiz (1971) changed the rank to subspecies. Subsequent authors have followed three different points of view: 1) Those who continued to consider it as a variety (Glassman, 1972 and Acevedo Rodríguez & Strong, 2012). 2) Those who placed it in the subspecies rank (Muñiz & Borhidi 1982, Moya & Leiva 2000, Govaerts & Dransfield 2005, Govaerts et al. 2011, Greuter & Rankin 2016). 3) Those who did not recognize its taxonomic validity and considered it as a synonym of *Coccothrinax miraguama* (Kunth) Becc. (Henderson, Galeano & Bernal 1995).

To designate the lectotype for *Coccothrinax miraguama* var. *arenicola*, priority was given to the materials cited in the protologue belonging to LS (currently in HAC), as it is the herbarium where Brother Leon worked during his entire professional stay in Cuba. It designated as lectotype *León 16146* [HACLS4387], on whose label León wrote "type." The numbers: *León 16147* [HAC-LS4386], used to describe flowers and *León 16148* [HAC-LS4385], remain only as paratypes. None of the seven duplicates of *León 16146,* in HAC-UO and US, had been previously been mentioned as part of the type material of *Coccothrinax miraguama* subsp. *arenicola* (León) Borhidi & O.Muñiz.

According to the above, the proposed nomenclature for the taxa analyzed is as follows:

Coccothrinax acuminata Becc., Webbia. 2: 313 (1907). *Thrinax acuminata* Griseb. & H. Wendl., in Sauvalle, Anales Acad. Ci. Med. Habana, 8: 563 (1871), *nom. nud.* Type. CUBA. [Provincia Artemisa, municipio San Cristóbal], Balestena. ft., 23. Feb. [1862 or 1864]. *Wright 3966* (lectotype, here designated, K 000462859 [photo!];

isolectotypes, here designated: BRU 55644 [photo!], BRU 55645 [photo!], V 92098F1 [photo!], V 92098F2 [photo!], V 92098F3 [photo!], FI 51879 ex K [photo!], GH 28253 [photo!], GH 28254 [photo!], GH 28255 [photo!], K 462858 [photo!], NY 73060 [photo!], NY 73076 [photo!], NY 73077 [photo!], NY 73078 [photo!], NY 73079 [photo!], P 725688 [photo!], P 725689 [photo!], US 87368 [photo!], US 87369 [photo!]).

Coccothrinax miraguama var. *novo-geronensis* Becc., Ann. Roy. Bot. Gard. Calcutta 13: 336 (1931). *Coccothrinax miraguama* [without rank] (*novo-geronensis*) Becc., Pomona Coll. J. Econ. Bot. 3: 409 (1913), **synon. nov**. Type. CUBA. [Municipio Isla de la Juventud], dry ground of poor quality near Nueva Gerona, Isla de Pinos, W.I., April [ft.]-1 May [fl.] 1904, *Curtiss 423* (lectotype, here designated, FI 051884 [photo!]; isolectotypes, here designated: CM 422028 [photo!], CM 422029 [photo!], G 305367 [n.v.], K 632580 [photo!], K 632581 [photo!], LE 793 [photo!], HAC!, M 208181 [photo!], MO 559592 [n.v.], MO 559593 [n.v.], NY 1661902 [photo!], NY 1662094 [photo!], NY 1662095 [photo!], NY 1662105 [photo!], US 14965 [photo!], VT117062 [photo!], MO 559592 [n.v.], MO 559593 [n.v.]).

Coccothrinax miraguama subsp. *arenicola* (León) Borhidi & O.Muñiz, Bot. Közlem. 58: 175 (1971). *Coccothrinax miraguama* var. *arenicola* León, Mem. Soc. Cub. Hist. Nat. "Felipe Poey'" 13: 114 (1939), **synom. nov**. Type: CUBA. [Provincia Pinar del Río, municipio Guane], sabana arenosa, hacienda Sabanalamar, El Sábalo (Pinar del Río), ft., 20. Aug. 1934, *León 16146* (lectotype, here designated, HAC-LS4387!; isolectotypes, here designated: HAC-UO1!, HAC-UO2! HAC-UO3!, US14992 [photo!], US14993 [photo!], US14994 [photo!], US14995 [photo!]).

Specimens examined: CUBA. Other specimens examined to which the identification is updated as *Coccothrinax acuminata*. The number of duplicates of each specimen in the same herbarium, is indicated in brackets.

Palmer 877 US [photo!]; *Shafer 299* HAC!, CM [photo! 3×], NY [photo! 2×]; *Baker 4808* HAC!, FI [photo!]; *Hermann 587* NY [photo!]; *Hermann 714* HAC!, FI [photo!]; *Hermann 839* HAC! [2×], FI [photo!]; *Jennings 156* NY [photo!], CM [photo! 2×]; *Jennings 623* CM photo!]; *Britton 6652* NY [photo! 2×], US [photo!]; *Britton 9748* NY [photo! 2×], US [photo!]; *Britton 10089* NY [photo! 2×]; *Britton 14227* CM [photo!], NY [photo!], US [photo! 2×]; Shafer 10561 NY [photo! 2×], US [photo!]; Shafer 10921 NY [photo! 2×], US [photo! 2×]; *Hermann 7909*, HAC! [5×]; *Hermann s.n.* HAC! [2×]; *León 16147* HAC!; *León* 16148 HAC!; León *16150* HAC!; *León 17034* HAC! [3×], US [photo! 2×]; *León 17035* HAC!, US [photo! 2×]; *León 17466* HAC!; *León 17467* HAC!; *León 18596* HAC!); *León 18734* HAC!; *León 18851* HAC!; *Killip 32239* US [photo! 2×]; *Acuña 19849* HAC! [2×]; *Alain 6913* HAC!; *Verdecia RV12/23* HMC [photo! 2×]; *Verdecia RV12/24* HMC [photo! 3×]; *Verdecia RV12/28* HMC [photo! 3×], NY [photo! 4×]; *Verdecia RV12/35* HMC [photo! 2×], NY [photo! 4×].

Notes: The species *Coccothrinax acuminata* belongs to subsection *Coccothrinax* of section *Coccothrinax*, according to the classification of Muñiz and Borhidi (1982), and Miraguama complex of the Pauciramosa Group, according to the informal classification of Nauman and Sanders (1991).

Distribution: Provinces Artemisa, municipality San Cristóbal; and Pinar del Río, municipalities Consolación del Sur, Guane, Mantua, Pinar del Río, Sandino, San Juan y Martínez y San Luis, (León 1939, Urquiola et al. 2001), and municipality Isla de la Juventud (León 1939).

Biogeography: Western Cuba subprovince, district *Guanahacabibense* (sector *Peninsularicum*), districts *Geronense, Indionense, Pinarense* and *Sabaloense* (sector *Pinaricum*) and district *Viñalense* (sector *Rosaricum*) (Borhidi 1996).

Habitat: The species grows in secondary savannas, seminatural savannas, coastal and subcoastal thorny shrublands and pine forest, on sandy-quartzite substrate, mainly on white sandy soils (Fig. 5 & Front Cover), alluvial soils and rarely on limestone.

Vernacular names: *Guanito* and *miraguano* (León 1939), *yuraguana* (González-Oliva et al. 2015).

Conservation status: Least Concern (LC) *sensu* González-Torres et al. (2016) for the categorization of *Coccothrinax miraguama* subsp. *arenicola*. According to González-Oliva et al. (2015), present in Guanahacabibes National Park, in the Los Indios and Los Pretiles Ecological Reserves, in the Sierra de Contadores-Cayo Ratones and San Ubaldo-Sabanalamar Managed Floristic Reserves, in the La Cañada Managed Resource Protected Areas and in the Península de Gunahacabibes Biosphere Reserve. León (1939) reported damage to populations by periodic fire and cutting by the *campesinos*, who use the leaves. González-Oliva et al. (2015) reported that it is used for rustic constructions.

Acknowledgments

We are grateful to Drs. Scott Zona and John Dransfield, who critically reviewed the manuscript. We acknowledge Paul Craft for his help and logistic contribution to the main author during fieldwork in the Isla de la Juventud and Pinar del Río, also for the translation into English. We thank Chiara Nepi of FI for sending us "The Palms of Odoardo Beccari." We thank Meghann S. Tonner and Ingrid Lin of US, Bonnie L. Isaac of CM, Walter Kittredge of A, GH, Chiara Nepi and Egildo Luccioli of FI, Tim Whifeld of BRU, and Banessa Falcón (LE and M) for making specimens available for study, to Dr. Rosa Rankin, from the National Botanic Garden of La Habana, for their advice regarding the application of certain articles of the ICN, and to Rafael Govaerts for his critical expert opinions on nomenclature.

LITERATURE CITED

ACEVEDO-RODRIGUEZ, P. AND M.T. STRONG. 2012. Catalogue of Seed Plants of the West Indies / Pedro Acevedo-Rodriguez and Mark T. Strong. Smithsonian Contributions to Botany 98. Washington D.C.

BECCARI, O. 1907. Le Palme Americane della Tribu delle Corypheae. Webbia 2: 1–343.

BECCARI, O. 1913. The palms indigenous to Cuba III. Pomona College Journal of Economic Botany 3: 391–417.

BECCARI, O. 1931. Asiatic palms–*Corypheae*: the species of the genera, revised and edited by U. Martelli. Annals of the Royal Botanic Gardens Calcutta 13: 1–344.

BORHIDI, A. 1996. Phytogegraphy and vegetation ecology of Cuba. Akademiai Kiado, Budapest.

BORHIDI, A. AND O. MUÑIZ. 1971. Combinationes novae Florae Cubanae. Botanikai Közlemenyek 58: 175–177.

BRITTON, N.L. 1910. Botanical Exploration in Western Cuba. Journal of the New York Botanical Garden 9: 226–236.

BRITTON, N.L. 1916. The natural vegetation of the Isle of Pines, Cuba. Journal of the New York Botanical Garden 17: 64–73.

BURRET, M. 1929. Palmae Cubenses et Domingenses a Cl. E. L. Ekman 1914–1923 lectae. Kung. Svenska Vetenskapsak. Hand. III. 6(7): 3–28.

CEJAS, F. AND P. P. HERRERA. 1995. El endemismo vegetal en las sabanas de arenas blancas (Cuba Occidental). Fontquería 42: 229–242.

CHIAPPY, C., L. MONTES, P. HERRERA AND R. CAPOTE. 1986. Estudio y valoración de la propuesta de Reserva Natural "La Cañada en la Isla de la Juventud. Reporte de Investigación del Instituto de Botánica 9: 1–24.

CUCCUINI, P. AND C. NEPI. 2006. The Palms of Odoardo Beccari. Quaderni di Botanica Ambientale e Applicata 17/1: 5–251.

DAHLGREN, B. 1936. Index of American Palms. Field Museum of Natural History Botanical Series 14: 1–456.

GLASSMAN, F. 1972. A revision of B. E. Dahlgren's index of American palms. Phanerogamarum Monographiæ, Tomus VI. Cramer, Lehre, Germany.

GÓMEZ DE LA MAZA, M. 1893. Nociones de Botánica Sistemática. A. Alvarez y Co., Habana.

GONZÁLEZ TORRES, L.R., A. PALMAROLA, L. GONZÁLEZ OLIVA, E.R. BÉCQUER, E. TESTÉ AND D. BARRIOS. (EDS.). 2016. Lista Roja de la Flora de Cuba. Bissea 10 (número especial 1): 1–352.

GONZÁLEZ-OLIVA, L., L.R. GONZÁLEZ-TORRES, A. PALMAROLA, D. BARRIOS AND E. TESTÉ. (EDS.) 2015. Categorización de taxones de la Flora de Cuba - 2015. Bissea 9 (número especial 4): 3–707.

GOVAERTS, R. AND J. DRANSFIELD. 2005. World Checklist of Palms. Royal Botanic Gardens, Kew.

GOVAERTS, R., J. DRANSFIELD., S.A. ZONA, D.R. HODEL AND A. HENDERSON. 2011. World Checklist of Arecaceae. Facilitated by the Royal Botanic Gardens, Kew. Published on the Internet; http://apps.kew.org/wcsp/ Retrieved 2016-07-27.

GREUTER, W. AND R. RANKIN. 2016. Espermatófitos de Cuba. Inventario preliminar. Parte II Inventario. Botanischer Garten und Botanisches Museum Berlin-Dahlem. Publicado en el Internet el 21 de junio 2016.

HENDERSON, A., G. GALEANO AND R. BERNAL. 1995. Field Guide to the Palms of the Americas. Princeton Univ. Press. Princeton, New Jersey.

Hernández, J., J. Á. Bastart, E. Medero and P. P. Herrera. 1995. Flora y vegetación de las sabanas de arenas blancas, Isla de la Juventud (Cuba). Estado de conservación. Fontqueria 42: 219–228.

Howard, R.A. 1988. Charles Wright in Cuba, 1856–1867. Chadwyck-Healy, Cambridge.

Jennings, O.E. 1917. A Contribution to the Botany of the Isle of Pines, Cuba, based upon the specimens of plants from that Island contained in the Herbarium of the Carnegie Museum under date of October, 1916. Annals of the Carnegie Museum 11: 19–290.

Jestrow, B., B. Peguero, F. Jiménez, R. Verdecia, L. González-Oliva, C.E. Moya, W. Cinea, M.P. Griffith, A.W. Meerow, M. Maunder and J. Francisco-Ortega. 2017. A conservation framework for the critically endangered endemic species of the Caribbean palm *Coccothrinax*. Oryx doi.org/10.1017/S0030605317000588.

León, Hno. 1918. Exploraciones Botánicas en Cuba. Memorias de la Sociedad Cubana de Historia Natural "Felipe Poey" 3: 178–224.

León, Hno. 1939. Contribución al estudio de las palmas de Cuba. III. Género *Coccothrinax*. Memorias de la Sociedad Cubana de Historia Natural "Felipe Poey" 13: 107–156.

León, Hno. 1946. Flora de Cuba 1. Gimnospermas. Monocotiledóneas. Contribuciones Ocasionales del Museo Historia Natural del Colegio de La Salle 8. La Habana. 441 pp.

McNeill, J., F.R. Barrie, W.R. Buck, V. Demoulin, W. Greuter, D.L. Hawksworth, P.S. Herendeen, S. Knapp, K. Marhold, J. Prado, W.F. Prud'homme Van Reine, G.F. Smith, J.H. Wiersema and N.J. Turland. 2012. International Code of Nomenclature for algae, fungi and plants (Melbourne Code) adopted by the Eighteenth International Botanical Congress Melbourne, Australia, July 2011.

Mejía, M. And R. García. 2013. Una nueva especie de *Coccothrinax* (*Arecaceae*) para la Isla Española. Moscosoa 18: 9–13.

Moya, C.E. and A. Leiva. 2000. Checklist of the palms of Cuba, with notes on their ecology, distribution and conservation. Palms 44: 69–84.

Moya, C.E., R. Verdecia, J.P. García-Lahera and L. Martínez-Pentón. 2017. The Coccothrinax azul from Sancti Spiritus, Cuba. Palms 61: 83–90.

Muñiz, O. and A. Borhidi. 1982. Catálogo de las palmas de Cuba. Acta Botanica Academiae Scientiarum Hungaricae 28: 309–345

Nauman, C. and R. Sanders. 1991. Preliminary classificatory studies in *Coccothrinax*. Selbyana 12: 91–101.

Novo, R., S. Aguilar, N. Suárez, J.L. Corvea, S. Perera, S.Y. Ulloa, Z. Acosta and L. González-Oliva. 2015. Plan de Manejo Reserva Ecológica Los Pretiles, Empresa Nacional para la Protección de la Flora y la Fauna.

Sargent, C.S. 1889. Some new or little known North American trees. Botanical Gazette 27: 81–94.

Sauvalle, F.A. 1871. Revisio Catalogi Grisebachiana vel Index Plantarum Cubensium. Anales de la Academia de Ciencias Médicas Físicas y Naturales de La Habana 7: 562–563.

Sauvalle, F.A. 1873. Flora Cubana (Sauvalle). Havana.

Schumann, K. 1901. VIII. Neue Arten der Siphonogamen 1899. Just's Botanischer Jahresbericht 27(1): 449–545.

Shafer, J.A. 1913. Further botanical explorations in Pinar del Río, Cuba. Journal of the New York Botanical Garden 14: 44–49.

Suárez, D. 2015. *Coccothrinax ×angelae* (*Arecaceae*), nuevo híbrido natural del género para Cuba. Revista Jardín Botánico Nacional Habana 36: 9–14.

Thiers, B. 2016. Index Herbariorum: A global directory of public herbaria and associated staff. New York Botanical Garden's Virtual Herbarium. http://sweetgum.nybg.org/science/ih/. Accessed 1 December 2016.

Underwood, L.M. 1905. A summary of Wright's exploration in Cuba. The Bulletin of the Torrey Botanical Club 32: 291–300.

Urquiola A., F.A. Urquiola, C. Ortega, O. Carriles, L. Chile, M.T. Del Toro, J.E. Rodríguez, L.R. Medina, C. Figueroa, I. Armas, A. Estrada, A. Rodríguez, C. Rivera, J.L. Roque, R. Novo, M. López, J.R. Aguilar, C. Cabrera, M. Betancourt and T. García. 2001. Levantamiento Florístico de la Provincia Pinar del Río. Informe de Proyecto. Delegación Territorial del CITMA Pinar del Río.

Verdecia, R. 2016. *Copernicia ×dahlgreniana*, a New Natural Hybrid in the Savannas of Camagüey, Cuba. Palms 60: 85–92.

The IPS is grateful for the support of the following patrons

2016

Platinum ($5000 and up)

Dr. Tom Jackson, California, USA, underwriting PALMS 61(1).

Ms. Jill Menzel, Florida, USA, in support of the Endowment Fund.

Gold ($1000 to $4999)

Ms. Sally Sneed Betts, Florida, USA,
in memory of her parents, Melvyn & Phyllis Sneed.

Mr. Leland Lai, California, USA.

Silver ($500 to $999)

Mr. Anthony Gray, Vancouver, Canada.

Bronze

Mr. Andrew Grant, California, USA.

Mr. Keith Thibodeaux, Louisiana, USA.

Dr. Lazaro Priegues, Florida, USA.

2017

Platinum ($5000 and up)

Ms. Jill Menzel, Florida, USA, in support of
the Larry Noblick Fund for Research.

Gold ($1000 to $4999)

Ms. Sally Sneed Betts & Ms. Sarah Morlang, USA,
in memory of their parents, Melvyn & Phyllis Sneed.

Silver ($500 to $999)

Palm Society of South Texas, USA

Bronze

If you would like to make a gift, however large or small, please contact IPS President Ray Hernandez, subtropicofcancer@hotmail.com or any IPS Board member. To give on-line, visit www.palms.org.