

The Stained-Glass Palm, *Geonoma epetiolata*



1. *Geonoma epetiolata* in the forest understory, Omar Torrijos National Park, Panama. Note contrasting colors of the expanding new leaf (yellow-purple) and the most recent mature leaf (green), both with substantial mottling.

MARIO A. BLANCO
*Department of Botany,
University of Florida,
220 Bartram Hall,
Gainesville, Florida 32611
USA*

*and
Jardín Botánico Lankester,
Universidad de Costa Rica,
Apdo. 1031-7050
Cartago, Costa Rica.
mblanco@flmnh.ufl.edu*

AND

SILVANA MARTÉN-RODRÍGUEZ
*Behavior, Ecology, Evolution
and Systematics (BEES),
Biology-Psychology Building
144,
University of Maryland,
College Park, Maryland
20742 USA
smartenr@umd.edu*

Geonoma epetiolata is the only neotropical palm that exhibits substantial leaf mottling. This article provides a summary of its biology and conservation, some observations of natural populations and a discussion of the ecological role of leaf mottling.

Palm leaves display a great morphological diversity; however, leaf color in most species is uniformly green. Color variation occurs in some species, in which the sheaths and petioles are red or orange (e.g., *Areca vestiaria*, *Cyrtostachys renda*), the adult leaves are covered with a bluish-gray bloom (e.g., *Brahea decumbens*, *Bismarckia nobilis*), the lower leaf surface is almost completely white (*Cryosophila* and *Arenga* spp.), or the new expanding leaves are bright red (e.g., *Actinokentia divaricata*, *Welfia regia*, *Calyptrocalyx* spp.). However, few species normally have truly variegated leaves.

In almost all palms with naturally variegated leaves, the variegation is expressed as mottling (roundish dark spots on a lighter background, or vice-versa; Dransfield 1974, Tucker 1992). This type of leaf variegation is well exemplified by various species of *Pinanga* and a few species and varieties of *Licuala*, both of them Asian and Malesian genera. But perhaps the most vividly colored foliage among variegated palms belongs to the Tropical American *Geonoma epetiolata*, the Stained-Glass Palm.

Described less than 30 years ago (Moore 1980), *G. epetiolata* remains relatively unknown despite its attractive foliage (Fig. 1). The few accounts of this species in the literature mention the unusual leaf pigmentation very briefly (Henderson et al. 1995, Ellison & Ellison 2001, Grayum 2003, Riffle & Craft 2003). The original description mentioned only the red or

purple lower surface of the leaves (Moore 1980). Only recently has some information about this species become available online (Gray 2006).

Distribution and habitat

The Stained-Glass Palm occurs in a few sites in Panama and Costa Rica. In Panama, populations are known from the provinces of Coclé, Colón, San Blas, and Veraguas. It is said that the type population north of Santa Fe de Veraguas has been extirpated by unscrupulous collectors, but this has not been verified by us. In Costa Rica, the Stained-Glass Palm is restricted to a narrow band of premontane rain forest that includes the northeastern part of Braulio Carrillo National Park and three adjacent private reserves. We have seen *G. epetiolata* in three locations: the private reserves Rara Avis and Terra Folia in Costa Rica, and in Omar Torrijos National Park in Panama (Fig. 2).

All known populations of *G. epetiolata* occur on the Caribbean slope at 300–1500 meters above sea level. In Braulio Carrillo National Park in Costa Rica, at least 37 other palm species, including eight species of *Geonoma*, occur at the same elevational band (Chazdon 1987).

Annual precipitation is very high at all the locations where *G. epetiolata* occurs. In Rara Avis private reserve for example, annual rainfall averages 6 to 7 meters, and more than

2. Caribbean slope of Cerro Calvario in Omar Torrijos National Park, Panama, one of the sites where the Stained-glass Palm occurs. Note the red, lateritic soil exposed by the dirt road.





3. New leaves are almost completely devoid of chlorophyll while expanding.

10 meters were recorded in 1997. This precipitation falls aseasonally throughout the year, although there are occasional dry spells. Even between rains the sky is almost always overcast. Consequently, the understory is generally very dark. The plants grow in the understory of primary forest on poor lateritic soils, but with abundant leaf litter on the soil surface.

Vegetative morphology

Plants of *G. epetiolata* have solitary brown stems that can (rarely) reach 2.5 meters in height, but most plants in a population are juveniles less than 1 meter tall. The diameter of the stem is 1–1.5 cm. About five to twelve leaves can be present at once, and the largest ones reach 60 cm in length. The leaves are

undivided, cuneate-oblongate in shape, and are bifid to almost one-fourth of their length (Figs. 1 & 3). Each bifurcation is acute at the tip, but when the leaves have not expanded completely the margins can be folded under, which creates the false impression of a rounded tip with an acuminate apex. The blades taper gradually towards the junction with the stem, where they form a short fibrous sheath without a connecting petiole (thus the specific epithet). The leaves are pleated between the veins, which run at a narrow angle relative to the midrib.

The leaves can be quite narrow, up to five times as long as wide. The type collection (*Dressler 4777*) has these narrow leaves. This seems to be an extreme of the variation, however, and



4. Only the youngest leaf shows the red underside. Notice three inflorescences, one with fruits.

the leaves can be proportionately wider, up to 2.5 times as long as wide; variation in leaf proportions has also been noticed by other observers (see Gray 2006). When fully expanded, young leaves appear wider than mature ones. During preparation of herbarium specimens the leaves seem to become somewhat narrower, probably because the plications become more pronounced after drying.

The most remarkable feature of the species is the beautiful color pattern of its foliage (Front Cover, Figs. 1 & 3). Young leaves are pale yellow with green veins, and marked with prominent red purple blotches over the upper surface. Frequently, but not always, the lower surface is flushed with red purple. The expanding leaves stand more or less erect, and when illuminated from behind they appear really luminous, like a pane of stained glass (thus the common name). Only the youngest leaf in each plant has these bright colors. Young leaves of *G. epetiolata* are similar to those of *Pinanga veitchii* (see back cover of *Principes* 34(2), April 1990), but the spots are red purple instead of brown.

As soon as they mature, the leaves turn into a beautiful light emerald green, and the spots

change from purple to dark green (Fig. 1). The texture of the upper leaf surface is not smooth but micropapillate, which gives it an opaque, velvety appearance. This combination of colors and texture make the mature leaves look like a thick pane of green sanded glass with dark stains at the opposite side. The red color frequently disappears from the underside of very old leaves, or from most mature leaves in plants exposed to bright light (Figs. 4).

Chazdon (1991) detected a correlation between plant size and degree of leaf complexity among species of *Geonoma*. Species with short stems tend to have small, undivided leaves, while taller species have progressively larger leaves with more divisions. Furthermore, for species with bifid (undivided) leaves, small leaves are more efficient than large ones in terms of shade tolerance (Chazdon 1986). *Geonoma epetiolata* fits this pattern well, as it is one of the smaller species in the genus. Its undivided, epetiolate leaves form something like a funnel, and dead vegetable matter frequently accumulates among the leaf bases of large individuals (Back Cover). Raich (1983) studied this phenomenon in *Asterogyne martiana*, another short understory palm with undivided leaves and very short petioles; he hypothesized



5. Few male flowers are produced per day on each spike.

the impoundment of debris is an adaptation to increase the quantity of nutrients available to the plant. When it rains, nutrients from the decomposing debris leach to the base of the stem and toward the roots.

Reproductive structures and phenology

Plants of *G. epetiolata* become reproductive at approximately 10 years of age (based on the average rate of leaf production and counts of leaf scars in the smallest reproductive plants seen). The unbranched inflorescences are borne from the leaf axils, and they can persist on the stem after the subtending leaf has fallen. One of us studied the reproductive biology of *G. epetiolata* in Costa Rica (Martén & Quesada 2001), and found that the spikes take from three to seven months to elongate completely after they emerge from their enclosing bract and prophyll. The rachis can reach 40 cm in length, and is held more or less erect at first (Fig. 4). Each spike starts with a male phase, and produces one to three staminate flowers per day for up to six months (Fig. 5). After all staminate flowers are spent the inflorescence enters the female phase (13 to 28 days), during which up to 25 pistillate flowers are produced each day. This extended flowering period per inflorescence is among the longest recorded for any palm species.

Each plant produces new inflorescences continuously, so that spikes in male, female and various fruiting stages often co-occur on the same plant. The plants are self-compatible, and they can be successfully fertilized with their own pollen (Martén & Quesada 2001). However, because staminate and pistillate

flowers are present on different inflorescences at any given moment, even self pollination has to be mediated by a pollinating agent.

Neither staminate nor pistillate flowers produce any nectar, and very few insect visitors were observed. Among these were weevils, drosophilid flies and stingless bees; none of them could be positively identified as a true pollinator. From 1020 flowers marked, only 13% initiated fruit and 75% of these aborted prematurely. Some abortions were caused by weevil predation (Martén & Quesada 2001).

After fertilization, the ovary swells and turns from yellow to green. The fruits ripen after five to nine months and turn dark purple. They are subglobose, about 0.6 cm in diameter. No animal dispersers were observed during the two-year phenology study, and many fruits simply fell to the ground after an average of 54 days on the inflorescence (Martén & Quesada 2001). This suggests that gravity is the main form of fruit dispersal, but it is likely that frugivorous birds also disperse some fruits. This low seed dispersal capability might explain why populations of *G. epetiolata* are so restricted geographically.

De Nevers and Grayum (1998) found that the populations east of El Copé (central-western Panama, where Omar Torrijos National Park is located) have female flowers with digitate staminodial tubes, whereas those to the west (including the Costa Rican one) have crenate staminodial tubes. Both morphs co-occur in El Copé. The degree of staminodial tube lobing in female flowers is taxonomically important in *Geonoma*, but this seems to be the only difference among eastern and western populations of *G. epetiolata* (de Nevers & Grayum 1998).

Why the leaf colors?

The micropapillate leaf texture and the abaxial anthocyanin layer on young leaves might represent adaptations to maximize the capture of photosynthetically active radiation (PAR) in the dark forest understory. Lee et al. (1979) demonstrated that the abaxial anthocyanin layer present in the leaves of many tropical understory plants reflects most of the PAR that has traveled through the leaf uncaptured by the photosynthetic pigments back into the mesophyll. *Geonoma epetiolata* grows in extremely low light environments, so its red leaf undersides are adaptive in this respect.

The abaxial layer of anthocyanins might also protect the photosynthetic pigments from the negative effects of ultraviolet radiation during

the formation of the new leaf (Gould 2004). However, this is unlikely to explain leaf coloration in an understory specialist such as *G. epetiolata*. An alternative explanation is that anthocyanins protect new leaves against fungal infections and insect herbivores (Coley & Barone 1989, Gould 2004).

Mottled leaves, even when attractive to the human eye, probably have the opposite desired effect: they can serve as camouflage. Most large mammal folivores of the forest floor (e.g., deer, tapirs, etc.) are color blind, and the mottling might hide the leaves from their sight by “breaking” their outline, so they “blend” with the background (Stone 1979, Givnish 1990, Tucker 1992) (Fig. 6). Another possibility is that the spots make the leaves appear diseased or senescent. In fact, most plants with naturally mottled foliage are short herbs of the forest understory, where they are more susceptible to defoliation by grazing mammal herbivores (Givnish 1990). All species of *Pinanga* with mottled leaves are understory palms; the species with the most strikingly mottled leaves in the genus, *P. veitchii*, is a very short plant, and larger species of *Pinanga* that have mottled leaves as juveniles lose some of the mottling intensity after they grow tall.

However, several epiphytes, notably some bromeliads, also have mottled or fenestrated foliage. Benzing and Friedman (1981) found that the dark spots on these bromeliads have higher concentrations of chlorophyll and likely have higher photosynthetic rates than the surrounding “pale” areas of the same leaf. They suggested that the patchy distribution of chlorophyll on the leaf optimizes the nutrient economy of the plant in a nutrient-poor environment and improves the light harvest of plants with multi-layered canopies in exposed situations. This hypothesis is also an unlikely explanation for the mottling in *G. epetiolata*, which occurs in the dark forest understory. Benzing and Friedman (1981) did not explicitly consider the potential role of leaf variegation as camouflage or disease mimicry as a defense against herbivory.

Most palms with mottled foliage tend to turn uniformly green when exposed to increased light levels (Tucker 1992). This provides further support for the understory camouflage hypothesis, because the mottling would be ineffective as camouflage in open areas, although Ferrero (2006) reported that the strongly mottled *Licuala mattanensis* can tolerate full sun. The camouflage hypothesis,

6. New leaves of *G. epetiolata* are very attractive to the human eye because of their colors (left). The same photograph in grayscale (right), approximates the vision of a color-blind mammal herbivore; notice how the mottling “breaks” the outline of the leaf and makes it harder to see against the background.



therefore, still awaits rigorous experimental testing (Allen & Knill 1991).

It is puzzling that no other neotropical understory palms have substantial leaf mottling (lowland populations of *Chamaedorea tuerckheimii* have a subtle mottling), while this phenomenon is more widespread among Malesian palms. Almost all of these, however, belong to the genus *Pinanga* (Dransfield 1974), which suggests this trait evolved only a few times among them.

Cultivation

The Stained-Glass Palm has never been common in cultivation, and has the reputation of being difficult to grow. A few small plants are grown successfully at Lankester Botanical Gardens in small pots with an organic mix and a generous layer of mulch on top. They should be kept under intermediate temperatures and high humidity and be watered daily. A couple of plants are in cultivation in the Atlanta Botanical Garden, where they are doing well planted in a highly organic mix designed for epiphytes. The species is reportedly in cultivation also in the Harold L. Lyon Arboretum (University of Hawaii at Manoa) and in a few private collections (Gray 2006).

In order to preserve the beautiful mottling and red undersides of the leaves, the plants should never be exposed to bright light, as already mentioned above. A few days of bright light (not even direct sunlight) will cause the leaves to turn almost uniformly green, and the affected leaves will not revert to the normal mottling even if the plant is returned to a shadier place (R. Determann, personal communication). Dransfield (1974) suggested that a nutrient-poor substrate could increase the intensity of the variegation in species of *Pinanga*, but this does not seem to be a requirement for *G. epetiolata*. Plants grow very slowly; populations in Costa Rica produce a new leaf approximately every three to six months (S. Martén-Rodríguez, unpublished data).

Geonoma seeds have a reputation for being difficult to germinate, and those of *G. epetiolata* are no exception. Several attempts to propagate the species in Costa Rica have consistently resulted in disappointingly low germination, although rigorous experiments to test the effects of different environmental conditions and scarification treatments have yet to be

carried out. Ellison and Ellison (2001) reported that seeds of this species can germinate within two to three months of planting, but gave no details about treatment.

Conservation status

The conservation status of *Geonoma epetiolata* has not been assessed before. Johnson (1996) listed this species in his Appendix 3 (Endemic palms with unknown conservation status) as being restricted to Panama, although as already said, it also occurs in Costa Rica.

At least in the two populations we have seen, the Stained-Glass Palm is locally abundant and protected within national parks and private reserves. Seedlings are not uncommon and there seems to be good recruitment. The condition of the other Panamanian populations is unknown to us. Habitat loss through deforestation is always a concern, given that there are so few known populations.

Like some other ornamental palms, the Stained-Glass Palm is threatened by collection of seedlings and adult plants for the horticultural trade (Johnson 1994). The owners of the private reserves in Costa Rica where the Stained-Glass Palm occurs are well aware of its presence, and they look after the population. Illegal collectors have been discovered on a few occasions. Given the slow growth rates of these palms and their low fruit set, any decrease in their populations can threaten the long term survival of the species.

Chazdon (1987) recommended seed germination studies for several ornamental palms in Costa Rica (including *G. epetiolata*) for propagation purposes, as a sustainable alternative to collection of plants from the wild. Johnson (1996) suggested that nurseries for propagation of ornamental palms should preferentially be established as close as possible to their natural populations, so the local people can acquire an appreciation of the palms, perceive a benefit from their presence in nature and feel compelled to protect them.

The area of occupancy of *G. epetiolata* in Costa Rica is estimated to be 50 km² (Martén & Quesada 2001), and the known populations in Panama probably occupy less than 150 km² altogether, taking into account the likely loss of habitat through deforestation. The extent of the species as a whole is likely declining. Given these circumstances, *G. epetiolata* should probably be listed as Vulnerable according to the IUCN Red List criteria (Johnson 1994, IUCN 2001).

Acknowledgments

We thank Ron Determann (Atlanta Botanical Garden) for information on his experience growing *Geonoma epetiolata*. Suggestions by John Dransfield and Robin Chazdon improved the manuscript. The Organization for Tropical Studies provided partial funding for the reproductive biology component of the research in Costa Rica by S. Martén-Rodríguez. Fieldwork in Panama and Costa Rica by M. Blanco was made possible by a U.S. National Science Foundation grant (DEB-0234064) to Norris H. Williams and W. Mark Whitten (Florida Museum of Natural History, University of Florida) for phylogenetic studies of subtribe Maxillariinae (Orchidaceae).

LITERATURE CITED

- ALLEN, J.A. AND R. KNILL. 1991. Do grazers leave mottled leaves in the shade? *Trends in Ecology and Evolution* 6: 109–110.
- BENZING, D.H. AND W.E. FRIEDMAN. 1981. Patterns of foliar pigmentation in Bromeliaceae and their adaptive significance. *Selbyana* 5: 224–240.
- CHAZDON, R.L. 1986. Physiological and morphological basis of shade tolerance in rain forest understory palms. *Principes* 30: 92–99.
- CHAZDON, R.L. 1987. The palm flora of Braulio Carrillo National Park, Costa Rica. *Brenesia* 28: 107–116.
- CHAZDON, R.L. 1991. Plant size and form in the understory palm genus *Geonoma*: are species variations on a theme? *American Journal of Botany* 78: 680–694.
- COLEY, P.D. AND J.A. BARONE. 1989. Red colouration of tropical young leaves: a possible antifungal defense? *Journal of Tropical Ecology* 5: 293–300.
- DE NEVERS, G. AND M.H. GRAYUM. 1998. Notes on *Geonoma* in Mesoamerica. *Principes* 42: 94–103.
- DRANSFIELD, J. 1974. Variegated Pinangas. *Principes* 18: 22–24.
- ELLISON, D. AND A. ELLISON. 2001. *Betrock's cultivated palms of the world*. Betrock Information Systems, Hollywood, Florida.
- FERRERO, M.D. 2006. More on *Licuala* horticulture. *PALMS* 50: 161,162.
- GIVNISH, T.J. 1990. Leaf mottling: relation to growth form and leaf phenology and possible role as camouflage. *Functional Ecology* 4: 463–474.
- GOULD, K.S. 2004. Nature's Swiss army knife: the diverse protective roles of anthocyanin in leaves. *Journal of Biomedicine and Biotechnology* 2004: 314–320.
- GRAY, M. 2006. *Geonoma epetiolata*. www.pacsoa.org.au/palms/Geonoma/epetiolata.html. Accessed 15 October 2006.
- GRAYUM, M.H. 2003. Areaceae. In B.E. Hammel, M.H. Grayum, C. Herrera, N. Zamora (eds.). *Manual de Plantas de Costa Rica*, Vol. II. Monographs in Systematic Botany from the Missouri Botanical Garden 92: 201–293.
- HENDERSON, A., G. GALEANO, AND R. BERNAL. 1995. *Field guide to the palms of the Americas*. Princeton University Press, Princeton, New Jersey.
- IUCN. 2001. IUCN Red List categories, version 3.1. IUCN Species Survival Commission. Gland, Switzerland, and Cambridge, U.K. (www.iucnredlist.org/info/categories_criteria2001).
- JOHNSON, D.V. 1994. The future of ornamental palms and the need for conservation. *Acta Horticulturae* 360: 121–127.
- JOHNSON, D.V. (ed.) 1996. *Palms: their conservation and sustained utilization*. IUCN, Cambridge.
- LEE, D.W., J.B. LOWRY, AND B.C. STONE. 1979. Abaxial anthocyanin layer in leaves of tropical rain forest plants: enhancer of light capture in deep shade. *Biotropica* 11: 70–77.
- MARTÉN, S. AND M. QUESADA. 2001. Phenology, sexual expression, and reproductive success of the rare neotropical palm *Geonoma epetiolata*. *Biotropica* 33: 596–605.
- MOORE, H.E. 1980. Two new species of *Geonoma* (Palmae). *Gentes Herbarum* 12: 25–29.
- RAICH, J.W. 1983. Understory palms as nutrient traps: a hypothesis. *Brenesia* 21: 119–129.
- RIFFLE, R.L., AND P. CRAFT. 2003. *An encyclopedia of cultivated palms*. Timber Press, Portland.
- STONE, B.C. 1979. Protective coloration of young leaves in certain Malaysian palms. *Biotropica* 11: 126.
- TUCKER, R. 1992. The phenomenon of mottled leaves in palms. *Palms & Cycads* 37: 6–13.

