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The growth form of *Phytelephas seemannii*—a potentially immortal solitary palm

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ABSTRACT

I studied the growth form of the vegetable ivory palm *Phytelephas seemannii* on the Pacific coast of Chocó, Colombia. The palm grows in the understory of riverine forests and has a large crown up to 16 m in diameter. The prostrate stem is erect for some distance at the apex and has abundant adventitious roots throughout its length. The palm differs from other plants having Corner's architectural model in that its stem often rots at the older end. Growing at the apex and dying at the base, the palm has no mechanical constraints to indefinite growth, and individuals can be potentially immortal. The creeping aspect of the stem is not due to plagiotropic growth but is the result of oblique orthotropic growth combined with gradual subsidence due to the crown's own weight, accumulated litter, or the impact of falling branches. This growth form is considered as the adaptation of a palm with a large crown to the understory of a frequently flooded forest. The same growth form is noted for the palm *Elaeis oleifera* and the cycad *Zamia roezlii*.

RESUMEN

Se estudió la forma de crecimiento de la palma de tagua *Phytelephas seemannii* en la costa Pacífica de Colombia. La palma crece en el sotobosque de selvas ribereñas y tiene una corona de hasta 16 m de diámetro. El tallo es postrado, erecto en el ápice, y está provisto de abundantes raíces adventicias en toda su longitud. La palma difiere de otras plantas que tienen el modelo arquitectónico de Corner, en que el tallo a menudo se pudre en el extremo basal. Creciendo en el ápice y muriendo en la base, la palma no tiene limitaciones mecánicas para un crecimiento indefinido, y los individuos pueden ser potencialmente inmortales. El aspecto rastrero del tallo no se debe a crecimiento plagiotrópico, sino que es el resultado de crecimiento ortotrópico oblicuo, combinado con una gradual reclinación debida al propio peso de la corona, a la hojarasca acumulada o al impacto de ramas que caen. Se considera esta forma de crecimiento como la adaptación de una palma con gran corona al sotobosque de selvas frecuentemente inundadas. Se señala el mismo hábito de crecimiento para la palma *Elaeis oleifera* y la cícada *Zamia roezlii*.

In spite of their overall architectural simplicity, palms exhibit a wide variety of growth forms (Holttum 1955, Dransfield 1978, Uhl and Dransfield 1987, Tomlinson 1990, Kahn and de Granville 1992). Four of the 23 architectural models described by Hallé et al. (1978) for trees are represented among palms: Corner's model (a solitary, unbranched, pleonanthic axis, as in the coconut); Tomlinson's model (axis branched at base, as in all clustering palms, individual axes being either hapaxanthic or pleonanthic); Holttum's model (a solitary, unbranched hapaxanthic axis, as in *Corypha*); and Schoute's model (dichotomously branched axes, as in *Hyphaene*). Although appropriate for describing the variation in architecture, the models do not describe aspects relevant to the ecological performance of palms, such as size, phyllotaxis, or overall growth form. Dransfield (1978) recognized four basic growth forms for palms, accounting for plant size: tree, shrub, acaulescent, and climbing palms. These categories, however, can hardly accommodate palms with prostrate or creeping stems. Uhl and Dransfield (1987) have briefly discussed the case of palms with prostrate stems, and Kahn and de Granville (1992) have treated them as a separate life form. In this paper, I describe the growth form of the vegetable ivory palm *Phytelephas seemannii* O. F. Cook, discuss its ecological significance, and compare it to that of other species with prostrate stems.

Phytelephas seemannii is a large, dioecious, solitary, understory palm with a thick stem up to 2–6 (occasionally up to 12) m long and 25 cm in diameter. Most of the stem lies on the ground, but its apical part is erect and up to 2–4 m tall. Leaf scars are densely arranged, and those of the lower side are hidden by numerous adventitious roots. The crown usually has 15–35 pinnate leaves to 8 m long and ca. 4.5 kg in weight. Female palms bear up to 20 infructescences in different developmental stages. The mature infructescence is spherical and compact, to 40 cm in diameter and weighs ca. 7 kg.

Phytelephas seemannii ranges from northwestern Colombia to Central Panama. It forms large homogeneous stands (Fig. 1) in the understory of riverine forests that are subject to brief flooding (Bernal and Ervik 1996) with an average density of 352 adult palms per hectare (Bernal, unpublished observations). This species was one of the former sources of vegetable ivory (Barfod 1989, Bernal 1992), and it is the basis of handicraft production in Panama (Dalling et al. 1996) and Colombia.

Materials and Methods

Stem length was measured in all adult palms in two 0.1-ha plots and in a plotless site ca. 0.3 ha (total *n* [number] = 201) at the Valle and Boroboro Rivers, in the Department of Chocó, on the Pacific coast of Colombia (5°34′–6°04′N, 77°20′–30′W). Sex and state of the stem base (whether complete or rotten above ground) were recorded for 320 palms along the Boroboro River. For palms having the base apparently undamaged above ground, underground rotting was not checked, as this would have required potentially destructive excavation. Height of the crown center from the ground was recorded for 120 palms along the same river. For 16 male and 18 female palms, the number of abrupt bends on the stem (reflecting past falls) was counted and the distance between bends measured; for these and 30 other palms in the area, stem shape and growth direction of the adventitious roots were studied in detail, in order to reconstruct the palm's past creeping history. Additionally, many casual observations were made during several years. Data from demographic plots (Bernal, unpublished observations) were used to describe the initial growth phase of the palm.

Results

Phytelephas seemannii has remote ligular germination (Fig. 2). The cotyledonary axis extends geotropically for 10–15 cm before the plumule emerges. The seedling produces three scale leaves (occasionally the upper one with a few reduced pinnae) before the plumule becomes evident (Bernal, unpublished observations). The eophyll has 14–18 pinnae on each side of the rachis, and successive leaves increase the number of pinnae. As the seedling grows, it produces an obconical, oblique stem (Fig. 3). The palm begins to produce an aboveground stem when it has already reached sexual maturity, at an approximate age of 24 years; at this point, the palm is still increasing the number of leaves in the crown (Bernal, unpublished observations). The stem initially grows orthotropically, either vertically or slightly leaning (Fig. 4), and in no case does it creep from its initial stages.

Totally vertical stems taller than 1 m are scarce. Only three individuals were observed in the study area with vertical stems 3–4 m tall; they all were males. As the palm grows, it often rotates the whole crown toward an area of higher light intensity, which is more evident near gaps or forest edges. Stems ca. 1.5–2 m long often exhibit a curved shape, the basal portion lying on the tangential side of the curve (Fig. 5). Stems ca. 2–3 m long are also curved, but they usually lie on the plane described by the curve (Fig. 6). Longer stems usually exhibit a range of patterns, from almost straight and creeping for most of their length, to variously meandering or describing a complete circle and with the apical portion erect (Fig. 7). These long stems are often marked at intervals by abrupt bends (Fig. 8) that contrast with their rather smooth curvature. Up to three such bends were found on the longest stems. These bends were closer to each other in females than in males (mean = 1.6 vs. 2.0 m, respectively; n = 22 females, 25 males; $F = 4.3$; $P = 6.8 \times 10^{-4}$). On average, males have longer stems than females (mean = 2.8 vs. 2.0 m; n = 105 males, 96 females; $F = 2.5$; $P = 3.8 \times 10^{-6}$), and the center of their crown is located higher than that of females (mean = 1.8 vs. 1.4 m; n = 60 males, 60 females; $F = 2.8$; $P = 5.1 \times 10^{-5}$). In 38% of all palms studied (n = 320), the stem was rotten at the base above ground. There was no significant difference between males and females in aboveground rotting at the base (P = 0.39). The longest stem recorded was that of a male 12.1 m long, the base of which was rotten. The stem of a 3-m-tall palm that was broken 1 m above ground by a falling tree at the river Arusí, fell to the ground and resumed growth after a few months, initially producing reduced leaves. Many palms that were cut down in a pasture at the Valle River were still growing several months later, although some others died.

Discussion

Phytelephas seemannii fits Corner's architectural model in having a single, unbranched stem with axillary inflorescences. Although palms conforming to this model have indefinite apical

1. A stand of *Phytelephas seemannii* at the Arusí River, Chocó, Colombia. 2–3. Early growth of *P. seemannii*. 2. A seedling showing remote ligular germination and first eophyll. 3. The subterranean stem of a juvenile ca. 15 years old, at the Valle River.

8. A *Phytelephas seemannii* with two straight stem segments and an abrupt bend (near the center of the photo), revealing at least two sudden falls. The stem was dusted with corn flour for contrast.

growth, there are mechanical constraints associated with stem size (Holttum 1955, Tomlinson 1990), and each particular palm species cannot exceed a certain size. Individuals must eventually die due to mechanical limitations. In *P. seemannii,* however, longevity is not conditioned by stem size. By losing the older portions at the base of the stem, the palm can keep within the mechanically functional limits of stem size. In this way, an individual may be potentially immortal because none of its tissues are ever too old. A similar pattern of growth is observed in the palm *Elaeis oleifera* (Jacq.) Cortés (Fig. 9), which occupies similar habitats to *P. seemannii,* and in the cycad *Zamia roezlii* Linden (Zamiaceae), which grows in mangroves on the Pacific coast of Colombia (Fig. 10). By growing at the apex and dying behind, these plants virtually move through the forest, probably being able, at least partially, to "discover" better light conditions. This departure from Corner's architectural model is so unique structurally and ecologically, that it should perhaps be recognized as an architectural model on its own.

The form and curvature of the stem allow one, in most cases, to trace the growth history of a particular individual. The process apparently begins from the seedling stage. Seedlings require forest gaps to grow into juveniles; thus, when an individual reaches adulthood, it is probably growing in or around an old gap. As the palm's stem grows obliquely, the crown rotates toward the area of higher illumination. As the lever arm on the rooting base increases, the palm gradually subsides. Because the palm apex always has orthotropic (although oblique) growth, the progressive sinking of the stem often results in an open curvature (Fig. 11a). When this process has advanced for a long time the base is often slightly risen from the ground. Rather than creeping (as a plagiotropic stem would do), the palm is almost rolling. If the torque caused by the crown is too strong, due either to its own weight (numerous developing infructescences), to litter accumulation, or to an impact by a falling branch, the crown will probably fall to the ground, and the stem will either uproot and rise (Fig. 11b) or break. Because uprooting (which seems to be more common) results in an unstable balance, the stem ends up lying on its side (Fig.

9. *Elaeis oleifera* near Juradó, Colombia. Note the rotten base of the stem.

11c). Evidence of this can often be seen by a change of direction of the adventitious roots. The stem recovers upright growth, and the process starts again (Fig. 11d). If the stem has risen to a height of 1 m or so when the crown falls next time, the older portion of curved stem that was lying on the ground may have risen to some height (Fig. 11e), if the stem does not break in the process. In some cases, the falls are probably instantaneous, as evidenced by the more or less abrupt bends on the stem (Fig. 8), which mark the point where the stem resumed apogeotropic growth. The fact that the bends are significantly closer in females indicates that they have abrupt falls more often than males. This is probably due to the weight of the numerous developing infructescences usually present on the crown, and it might explain why female crowns reach a lower height on average than males. It probably accounts also for the shorter stems in females: If female stems fall more often, they have a higher risk of breaking during an abrupt fall, and have more portions exposed to being covered by flooding.

The falls are probably not always instantaneous, as evidenced by the occurrence of many stems lacking abrupt bends. In such cases, the smooth curvature of the stem is probably the result of gradual subsiding, combined with orthotropic growth of the stem and probably also with the rotation of the crown toward changing light conditions in the forest canopy.

For the American oil palm *Elaeis oleifera*, which has the same growth form, Tomlinson (1990) considered that the gradual subsidence of the stem may be only apparent, and that the reverse is what happens: the initially horizontal apex becomes erect. My observations on this species (Fig. 9) indicate that the process is identical to that of *P. seemannii*, and that gradual subsidence occurs. Casual observations of the cycad *Zamia roezlii* (Fig. 10) suggest that it also grows in the same way. Other palms described as having creeping stems, e.g., *Johannesteijsmannia altifrons*, *Licuala* spp. (Uhl and Dransfield 1987), *Chelyocarpus repens* (personal observations, Kahn and Mejía 1988, Kahn and de Granville 1992), *Nypa fruticans* (Tomlinson 1990) or *Serenoa repens* (personal observations, Fisher and Tomlinson 1973, Tomlinson 1990) differ in having plagiotropic development, and are therefore true creeping palms. Rotting of the older portions of the stem in these species has been documented only for *Licuala* spp. (Saw Leng Guan, personal communication) and for very old plants of *Serenoa repens* (J. B. Fisher, personal communication), and it apparently occurs also in *Johannesteijsmannia altifrons* (Uhl and Dransfield 1987).

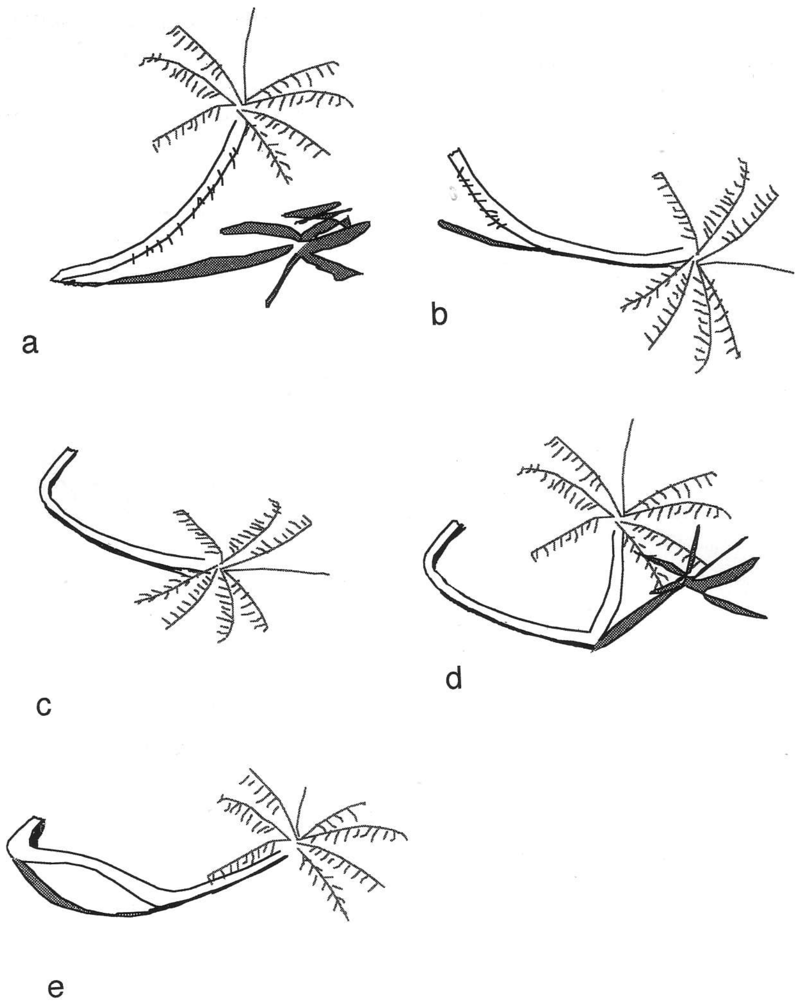
The ability of *P. seemannii* to resume growth after its stem has been broken is rare in the palm family, and it can be explained by the abundant adventitious roots present all along the stem. In most other palms, adventitious roots are confined to the basal portions of the stem (Tomlinson 1990). The occasional failure of individuals of *P. seemannii* to recover from a stem rupture is probably associated with the season of the event, and the length of the stem portion that remains attached to the crown (Bernal, unpublished observations). If a stem is broken during the dry season or is cut very close to the crown, the available roots probably will not be enough to cover the water stress.

The growth form of *P. seemannii* is not only unusual in the palm family, but also within the genus *Phytelephas*. It probably represents the

10. A young individual of *Zamia roezlii* at the Pacific coast of Colombia. Note the rotten stem base.

optimal growth form for a large palm (crown up to 16 m in diameter) of the forest understory, in an area where the high rainfall (5000–7000 mm per year) does not favor the development of a subterranean stem on river banks, due to the high water table. This is supported by the fact that in drier areas in Panama this species is often acaulescent or has a stem up to 1 m tall (Dalling et al. 1996); also, its closest relative, *P. macrocarpa* ssp. *schottii*, of the Magdalena River basin in Colombia, usually has a subterranean stem when it grows on drier slopes (Barfod 1991), but populations growing on the alluvial plains have the same growth form as *P. seemannii* (Claés 1925). The fact that the two other plants reported here as having the same growth form as *P. seemannii*, viz. *Elaeis oleifera* and *Zamia roezlii*, both also have large crowns, grow in areas with high water table, and have relatives with subterranean stems growing in drier areas also supports this view. *E. oleifera* has a crown as large as that of *P. seemannii* (both palms are strikingly similar, Fig. 9), and grows in swampy or frequently flooded areas (Vallejo Rosero 1976, Kahn and Mejía 1986); its closest American relative, *Barcella odora*, is a palm of the sandy soils in the campinaranas north of the Rio Negro in Brazil, and has a subterranean stem (Henderson 1986). *Z. roezlii* (Fig. 10) has perhaps the largest crown of any South American cycad, up to 6 m in diameter and with up to 30 leaves, abounds in mangrove swamps (personal observations, Norstog 1986), and has many close relatives with subterranean stems. The fact that the three species are dominant elements of the understory in their respective areas bespeaks the ecological success of this growth form.

Phylogenetic analysis of the subfamily Phytelephantoideae (Barfod 1991) has shown *P. seemannii* and *P. macrocarpa* as the most derived species in the genus. *P. macrocarpa* ssp. *schottii* is endemic to the Magdalena River valley in Colombia and, as mentioned above, it exhibits both subterranean and aerial, oblique, partially prostrate stems depending on the habitat. Thus, I hypothesize that migration of *P. macrocarpa* (or of its acaulescent ancestor) from northwestern Amazonia into the wetter areas of the Magdalena River valley before the upheaval of the Colombian Eastern Cordillera, and further west into



11. Schematic representation of the growth form of *P. seemannii.* (a) Orthotropic growth combined with progressive sinking of the stem often results in an open curvature. (b) A sudden fall uproots and raises the stem base. (c) Because balance of b is unstable, the stem ends up lying on its side. (d) The stem resumes upright growth. (e) The crown falls again, and the older portion of curved stem that was lying on the ground is raised slightly.

the Chocó, giving rise to *P. seemannii,* entailed the ability to develop an aerial stem provided with abundant adventitious roots. Frequent flooding and strikes of falling branches and trees on the easy target offered by the large crown must have acted as strong selective pressures for this growth form.

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(Continued from p. 8)

Everywhere there were palms, many growing submerged in water along the river margins, others growing in swampy upland conditions, but most were located on terra firme sandy loam soil. Climatically it was hot but not oppressive. Fortunately there were few mosquitoes on the tannin-stained waters of the Rio Negro, as its strong acidity apparently inhibits heavy mosquito breeding. Although the area was sparse in population, we visited several villages and isolated thatched homes of the local Portuguese-speaking caboclos, several of whom guided us to palm-growing sites and sold us fish, including piranhas, etc., which we later cooked on board.

Traveling northwestward on the Rio Negro we cruised as far as the confluence of the smaller Rio Padauari and the Rio Negro, almost the head of navigation for a craft of our draft, as further upstream rapids prohibit onward navigation. Altogether, we traveled up the Rio Negro eight days before reversing course downstream where after two days and two nights we were back in Manaus for a last day of sightseeing. Throughout our trip on the river we were accompanied by the famed pink Amazonian dolphins, which continually swam and leaped around us in friendly curiosity.

Our final count of palms was 18 genera and 55 species, the most outstanding of which were: *Astrocaryum jauari* (clumping, fruits eaten by fish), *Astrocaryum paramacca* (uncommon on the Rio Negro), *Attalea racemosa* (trunkless), *Bactris bidentula* (a probable rheophyte), *Bactris campestris* (flat leaf spines), *Bactris riparia, Barcella odora* (highlight, a rare sight), *Desmoncus polyacanthos, Euterpe catinga* (orange crownshaft), *Geonoma stricta* (blue fruits), *Leopoldinia major* (clumping in deep water), *Leopoldinia piassaba* (rare, drooping fibers), *Lepidocaryum tenue* (understory, scaled fruit), *Manicaria saccifera* (huge leaves, warty fruits), *Mauritia carana,* and *Mauritiella aculeata.* There were of course many more, far too numerous to mention.

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4–7. Stem bending in *Phytelephas seemannii.* 4. A female palm with leaning stem. 5. A stem resuming upright growth after falling to the ground. 6–7. Two palms with different stem lengths. The stems were dusted with corn flour for contrast.