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STRANGULATION OF THE PALM *PHYTELEPHAS SEEMANNII* BY THE PIONEER TREE *CECROPIA OBTUSIFOLIA*: THE COST OF EFFICIENT LITTER TRAPPING

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Resumen. Estudiamos la captura de hojarasca en la corona de la palma del sotobosque *Phytelephas seemannii* en la Costa Pacífica del Chocó, Colombia, y el subsiguiente estrangulamiento de la palma por el árbol pionero *Cecropia obtusifolia*. La gran corona de la palma captura hojarasca y la dirige hacia las axilas de las hojas, donde el tallo produce abundantes raíces adventicias. Aunque la palma sólo captura hojarasca producida por encima de 3–6 m sobre el suelo, el centro de la corona recibe hasta tres veces más hojarasca pequeña que la que recibiría sin arquitectura captadora de hojarasca. Con una densidad promedio de 352 palmas por hectárea, la población de *Phytelephas* captura alrededor del 8 % de toda la hojarasca producida en un área determinada. La hojarasca atrapada incrementa los nutrientes disponibles para la palma y alberga numerosas especies de artrópodos, especialmente hormigas y termitas, que probablemente aportan nutrientes adicionales. El humus producido en la corona de la palma es más rico en la mayoría de nutrientes que el suelo en la base de la palma o cerca de ella. Las raíces de varias especies de árboles, principalmente *Cecropia obtusifolia*, se encontraron en la corona de un 5 % de todas las palmas estudiadas. Si las raíces de *Cecropia* alcanzan el centro de la corona, aprietan las hojas jóvenes y las hojas bandera y finalmente la palma muere, probablemente como consecuencia de la reducción en la conducción de agua y nutrientes hacia las hojas y por la falta de espacio del meristemo apical para seguir creciendo. Las muertes están asociadas con la formación de claros en el dosel en los 10–37 años anteriores. Se estima que la tasa anual de estrangulamiento es del orden de 1 en 10^4 individuos, y probablemente sólo es superada en importancia, como causa de mortalidad, por la migración de los canales de los ríos.

Abstract. We studied litter trapping by the crown of the understory palm *Phytelephas seemannii* at the Pacific coast of Chocó, Colombia, and the subsequent strangulation of the palm by the pioneer tree *Cecropia obtusifolia*. The large crown of the palm captures litter and funnels it into the leaf axils, where the stem produces abundant adventitious roots. Even though the palm captures only litter produced higher than about 3–6 m above the ground, the crown center receives up to three times as much litter as it would without a litter-trapping architecture. With an average density of 352 palms per ha, the *Phytelephas* population captures about 8 % of all the small litter produced in a given area. The trapped litter increases the nutrients available to the palm and harbors numerous species of arthropods, notably ants and termites, which probably contribute additional nutrients. Humus produced in the palm crown is richer in most plant nutrients than the soil at the base of the palm and nearby. Roots of several tree species, notably *Cecropia obtusifolia*, were found in the crown of 5 % of all adult palms studied. If the roots of *Cecropia* reach the center of the crown, they will grow around and strangle the young leaves and the spear leaves and will eventually kill the palm, probably because water and nutrient conduction to the leaves is reduced, and the apical meristem lacks space to grow. Deaths are associated with gaps 10–37 years old. Annual death rate by strangulation is estimated to be in the order of 1 per 10^4 individuals. After river channel migration, this is probably the most important cause of adult palm mortality. *Accepted 26 December 1996.*

Key words: Cecropia obtusifolia, *Chocó, Colombia, litter trapping,* Phytelephas seemannii, *stranglers.*

INTRODUCTION

Litter fall represents a major pathway in the nutrient cycling of rainforest ecosystems (e. g., Vitousek & Sanford 1986). Litter interception can therefore be an efficient means for understory plants to gain access to nutrients, and selection is expected to favour litter-trapping architecture in plants having the appropriate size and mechanical structure. Litter-trapping plants (referred to as detritophilic) commonly have palmoid growth-forms (Ng 1980, Parker 1994), and palms are indeed the most obvious detritophilic plants. Litter trapping has been recorded for many understory species of palms (de Granville 1977, Raich 1983, Holbrook *et al.* 1985, Putz & Holbrook 1989, Dransfield & Beentje 1995), and it has been suggested that litter-trapping palms contribute substantially to forest litter distribution

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(Kahn & de Granville 1992). In *Asterogyne martiana*, stem-flow is richer in nutrients than either throughfall or rainfall, and it has been suggested that *Asterogyne* palms in a sense fertilize themselves (Raich 1983). Putz & Holbrook (1989) found that the humus accumulated among the persistent leaf bases of *Copernicia tectorum* in the Venezuelan Llanos is higher in nutrients than soil from the ground near the palms; at that study site *Copernicia* palms were the predominant hosts for strangler figs, but usually the figs did not kill the palms, although their roots were abundant among the accumulated humus.

This paper discusses litter trapping by the palm *Phytelephas seemannii* O.F. Cook, and how litter trapping indirectly leads to its strangulation by the pioneer tree *Cecropia obtusifolia* Bertol. The impact of strangulation on the palm population is estimated.

MATERIALS AND METHODS

Study species. Phytelephas seemannii is a large understory palm with a solitary, thick, decumbent stem up to 10 m long and 25 cm in diameter. Its apical, erect portion ascends to 2–3 m above the ground. Leaf scars are densely arranged on the stem, those on the lower side being hidden by numerous adventitious roots. Along the upper, ascending part of the stem the adventitious roots are short (up to 10 cm) and covered by the decaying leaf bases. The crown has on average 20 pinnate leaves that are 5–8 m long; dead leaves do not abscise cleanly but persist on the stem, breaking and disintegrating in time. The great length of the leaves, combined with the high density of the nearly monospecific understory palm stands, implies that the foliages of adjacent palms often overlap, making a canopy at about 3–6 m above the ground that strongly shades the forest floor (Fig. 1). Because most of the leaves are ascendant, the palm crown acts as an efficient trap that funnels litter toward the leaf bases, where it accumulates (Fig. 2). This litter and the resulting humus attract different species of animals and roots of neighboring trees.

Cecropia obtusifolia (Cecropiaceae) is a widespread tree in Central and South America (Berg & Franco Roselli 1993) and is the commonest of the *c.* five *Cecropia* species in the study area. It is an abundant pioneer tree along river margins, reaching 25 m in height and 25–30 cm in diameter. To date, apparently neither this species nor any other in the genus has been reported as a strangler.

Study area. The study was carried out in the Department of Chocó, Colombia, on the flood plain of Boroboro River, 5 km inland from the Pacific Ocean (6°04'N, 77°20'W); additional observations were made on the Valle and Arusí Rivers, 5 km north and 60 km south, respectively, of the main study site. The area is covered by undisturbed or slightly disturbed tropical wet forest, 0–10 m a.s.l. Rainfall in the area is about 5000 mm per year, and annual mean temperature is 26°C (unpublished data at IDEAM, Bogotá). On the alluvial river plains that are subject to brief flooding throughout most of the year, the forest understory is dominated by the palm *Phytelephas seemannii*, which usually forms large, homogeneous, nearly monospecific stands. The Boroboro River harbours the best-preserved palm stands.

Density. We determined adult palm density in five 0.1 ha (20 x 50 m) plots: three on Boroboro River, and two on Valle River.

Litter accumulation rate. Litter accumulation rate was determined by removing all small litter (leaves, reproductive parts, twigs, and branches ≤ 2.5 cm) from 20 palms in November 1995 and collecting and weighing new accumulated litter 3.5 and 7.7 months later. Dry weight of the litter was determined by thoroughly mixing all material collected from one palm and taking a sample of it; this sample was weighed, dried at 70°C for 72 hours, and weighed again.

Standing stocks of litter. The amount of litter and humus present among the leaves and leaf bases was determined by collecting and weighing all accumulated organic matter from 10 palms, and determining their dry weight as described above.

Ants, termites and tree roots. Presence of ants, termites and tree roots among the litter and humus was determined for all adult palms in two 0.1 ha plots (n = 80) and for 400 adult palms along a transect 8 m wide and *c.* 1.5 km long.

Nutrient analysis. Soil samples for macronutrient analysis were taken from the humus accumulated among the leaf bases of seven palms, from the upper 10 cm of soil at the base of each palm, and from 3 m away from the base of the palm. Soil analyses were made by the Soil Laboratory of the Universidad Nacional de Colombia, Bogotá. Soil pH was determined in volumetric 1:1 and 1:2 water solutions; organic carbon by the Walkley-Black method; total nitrogen by the Kjeldahl method; available phosphorus by extraction with the Bray II method; exchangeable cations were extracted with 1N ammonium acetate at pH 7 and determined by atomic absorption. For micronutrient analysis samples were taken from three palms as described above. These samples were analysed by the Soil Laboratory of the Instituto Geográfico Agustín Codazzi in Bogotá. Manganese, iron, zinc, and copper were extracted by the double acid method and determined by atomic absorption; boron was extracted in hot water and determined colorimetrically.

Strangling. All palms killed by *Cecropia*, or *Cecropia* trees showing evidence of having killed a palm (i. e., trees with a cylinder of roots in place of the palm stem), were recorded in six 0.1 ha plots and in the transect (total n = 620). For all living *Cecropia*-bearing palms in the transect, and for other strangled palms outside the transect, the position of the roots on the palm stem was noted, and height and stem diameter of the *Cecropia* (diameter at 1.3 m from its rooting position) was measured. All leaves were removed from an near-killed palm in order to determine the position of the uppermost *Cecropia* roots.

Litter production. Because no litter fall data are available for the study area, Brown & Lugo's (1982) formula was used to estimate the overall litter production of the forest:

$$L = 16.0 + 16.7 \log(T/P) - 6.5\ (T/P),$$

where L is annual litter fall in tonnes per ha per year and T/P is the ratio between annual mean temperature (°C) and annual rainfall (mm), multiplied by 100. This equation predicts an annual litter fall of 7.8 tonnes per ha per year.

RESULTS

Density in the *Phytelephas seemannii* stands was 240–420 adult palms per ha ($\bar{x}$ = 352; SD = 70.5). Rate of litter trapping averaged 148 g per month (SD = 75), and the total amount of dry matter accumulated at a given time in the crown averaged 4.5 kg per palm (SD = 1.6).

The soil nutrient analysis showed that humus accumulated among the leaf bases was richer in organic matter and in several plant nutrients, including micronutrients, than soil at the base of the palms and nearby (Table 1). Soil samples from the base of the palms also had higher concentrations of some

FIG. 1. A stand of *Phytelephas seemannii* at the Boroboro River, Chocó, Colombia.

FIG. 2. Litter accumulated in the crown of *Phytelephas seemannii.*

nutrients than soil collected 3 m away, but the differences were not significant.

Ants and termites were the most abundant animals in the crowns of all palms examined. There were ants on 32.5 % of the 480 palms in the two 0.1 ha plots and the 8 m x 1500 m transect. Eight species of ants were identified in the palm litter (Table 2); the commonest and most abundant was *Odontomachus bauri,* which was present in 28.3 % of all palms. We observed this species preying on termites. Twenty percent of the palms studied had termites of the genus *Nasutitermes,* which built covered runways on the dead, persistent leaves. Nests were uncommon in the palms (0.8 %).

In the transect, twenty palms (5 % of all adults) had tree roots growing into the accumulated humus. Three species of trees were involved. The most abundant tree was *Cecropia obtusifolia,* which was recorded on 15 palms (3.8%) in the transect. *Sapium laurifolium* (Euphorbiaceae) had roots on three palms, and *Trichilia* sp. (Meliaceae) on two. In other sites outside the transect, another species of *Cecropia,* a species of *Ficus,* and an unidentified Lauraceae were recorded with roots around adult palms.

TABLE 1. Soil nutrient content of humus accumulated in the crowns of *Phytelephas seemannii* palms, of soil collected at the base of each palm, and of soil collected from 3 m away from the palm bases (macronutrients, n=7; micronutrients, n=3). Means are followed by standard deviation in parenthesis. The F-test and the probability (P) values are for comparisons between nutrient content in the epiphytic humus and at the palm base.

Variable	Humus (SD)	Palm base (SD)	3 m from base (SD)	F	P
pH	5.3 (0.37)	5.5 (0.18)	5.5 (0.18)	2.2	NS
% organic C	8.7 (3.70)	2.5 (0.58)	1.8 (0.59)	19.2	< 0.001
% N	0.88 (0.15)	0.21 (0.05)	0.15 (0.05)	116.5	< 0.001
C/N	10.2 (3.98)	11.8 (0.18)	12.0 (0.27)	1.2	NS
P (ppm)	16.6 (7.87)	2.0 (0.58)	2.3 (1.11)	23.9	< 0.001
K (meq/100 g)	0.88 (0.19)	0.63 (0.19)	0.63 (0.16)	5.0	< 0.05
Mg (meq/100 g)	11.9 (2.85)	13.1 (1.7)	13.9 (7.19)	0.94	NS
Ca (meq/100 g)	59.9 (24.39)	35.2 (5.89)	31.4 (2.61)	6.8	< 0.05
Na (meq/100 g)	3.9 (1.92)	3.8 (2.0)	3.4 (2.06)	0.002	NS
CEC	65.1 (22.03)	43.6 (7.37)	41.6 (6.88)	6.02	< 0.05
Mn (ppm)	60.0 (25.85)	28.4 (5.50)	19.1 (0.83)		
Fe (ppm)	207.3 (98.8)	108.3 (16.03)	95.3 (16.42)		
Zn (ppm)	14.5 (7.54)	2.1 (0.40)	1.57 (0.42)		
Cu (ppm)	16.1 (9.43)	10.7 (0.55)	9.9 (1.16)		
B (ppm)	0.39 (0.21)	0.07 (0.04)	0.06 (0.02)		

TABLE 2. Species of ants found among litter accumulated in the crown of *Phytelephas seemannii* in Chocó, Colombia.

Species	Subfamily
Odontomachus bauri Emery	Ponerinae
Paraponera clavata Fabricius	Ponerinae
Megalomyrmes aff. *modestus* Emery	Myrmicinae
Wasmannia cf. *auropunctata* (Roger)	Myrmicinae
Dolichoderus ferrugineus Forel	Dolichoderinae
Linepithema cf. *humile* (Mayr)	Dolichoderinae
Camponotus cf. *renggeri* Emery	Formicinae
Paratrechina nodifera (Mayr)	Formicinae

Cecropia seeds may germinate directly on the palm stem, but most seedlings and juveniles associated with *Phytelephas seemannii* were growing on the ground and extended prop roots into the humus collected by the palm. All individuals of *Cecropia* that embraced palms were adults 9–25 m tall and 12–28 cm diameter. In all cases the roots encircled the upper 1.5 m of the stem (Fig. 3A). All 14 living *Cecropia*-bearing palms in the transect looked healthy and showed no evidence of injury; 13 of them had inflorescence buds or fruits. In all cases, the roots of the *Cecropia* had not reached the center of the crown, and they were winding among the old leaf bases only. Four individuals found outside the plots or the transect had severe signs of strangulation, with *Cecropia* roots strongly holding together the youngest 5–10 leaves; signs of strangulation included progressive reduction in size of the youngest leaves, drying of the younger leaves and the spear leaf, and complete drying of all leaves, including the spear leaf. In all four cases the cecropias had stems ≥ 18 cm in diameter.

Within the transect, one palm (0.25 % of all individuals) killed by *Cecropia* was found. Strangulation had apparently happened within the past year, because leaf remnants were still in evidence. Another strangled palm was found in one of the six 0.1 ha plots (0.45% of all individuals). This individual had probably been killed several years before, since the stem was severely decayed.

DISCUSSION

Efficiency of *Phytelephas* as a litter trap can be determined by relating litter captured by the crown to estimates of litter fall in the forest. Litter accumulates in the crown of *P. seemannii* in a roughly circular area *c.* 1 m across (Fig. 2), i.e. a surface of *c.* 0.785 m^2. Thus, the average monthly litter accumulation of 148 g per palm represents 2262 g per m^2 per year. This figure is about three times as much as the value predicted for the study site, and 1.8 to 3.4 times as much as the values of small litter fall listed by Duivenvoorden & Lips (1995) for 30 tropical rainforest sites throughout the world. Thus, the *Phytelephas* crown can be estimated to capture about 2–3 times as much litter as it would if it had a non-detritophilic architecture, even though it captures only litter produced above a height of 3–6 m. With an average density of 352 palms per ha, the adult *Phytelephas* population captures about 8 % of all litter produced in a given area, although its basal area accounts for only 0.17 % of a hectare.

Arthropods no doubt contribute nutrients to the humus. The most important sources of nutrients are probably termites and ants. Carton-nest termites are well-known nitrogen contributors and their nests have been found to be richer in nutrients than adjacent soil or epiphytic humus (Prestwich *et al.* 1980, Salick *et al.* 1983, Putz & Holbrook 1989). Ants, particularly the large colonies of the predatory *Odontomachus bauri* which were commonly found in the palms, probably accumulate significant amounts of nutrients by excreting nutrient-rich feces (Raich 1983).

The nutrient trapping mechanism of *P. seemannii* differs from that of most other detritophilic palms in that the palm is auto-epiphytic (Ng 1980), i. e., it is "rooted" in the mass of humus accumulated in its own crown. In this respect it resembles the litter-trapping *Elaeis oleifera* (Patiño 1977), which also has the same growth-form as *P. seemannii* (pers. obs.), and the Malagasy *Masoala madagascariensis*, which has an erect stem 3.5–10 m tall (Dransfield & Beentje 1995). Both of these species are massive palms with thick stems and large, marcescent leaves. Most other litter-trapping palms lack adventitious roots high on the stem, and nutrients in throughfall and in trapped litter are probably diverted along the stem directly to the rooting zone, as in the small-statured species *Asterogyne martiana* (Raich 1983). Whereas keeping large amounts of litter in the crown until it decays into humus may be a more effective means of capturing nutrients than just leaching them from gross litter, it also poses the risk of being invaded by alien roots.

The fact that trees in five unrelated plant families were found with their roots growing into the epiphytic humus of *Phytelephas* suggests that the accumulated humus can be used by any tree roots that are close enough to follow a nutrient gradient. But humus accumulation only takes place after there is an above-ground stem, when the persistent leaf bases retain the litter until it decays completely. Thus, as the nutrient gradient probably increases with stem growth, it also becomes more difficult for tree roots to grow apogeotropically along the gradient, particularly if the lower portions of the stem become naked. That is probably why *Cecropia* predominates as a strangler of *Phytelephas*. First, the prop roots of *Cecropia* can reach the humus directly, without having to grow apogeotropically. And second, *Cecropia* abounds in gaps, where palms are often knocked down by falling trees or branches, bringing their mass of humus close to the ground. Young palms which have not yet developed an above-ground stem also trap litter, but they do not have a mechanism for retaining it for a long time; thus, trapped litter is finally funnelled to the ground, and the palm does not accumulate substantial amounts of humus. That might explain why young *Phytelephas* (or large acaulescent palms like *Attalea allenii*) do not have tree roots growing around their crowns.

In most cases, cecropias apparently do not begin their lives as hemiepiphytes, but they invade the crown after germinating on the ground. This makes sense, considering that there are far more chances for the small *Cecropia* seeds to reach the soil than the crown humus. Thus, when a palm is knocked down in the process of gap formation, there will probably be more *Cecropia* seeds on the ground around the palm that within the crown itself. Field observations support this: only in one case was a *Cecropia* seedling found growing on a palm stem, whereas seedlings and saplings were abundant on the ground near palms fallen in gaps, with their roots invading the crown or growing toward it. Fourteen out of 15 cecropias found on palms in the transect were adults ≥ 12 cm dbh.

FIG. 3. Strangulation of *Phytelephas seemannii* by *Cecropia obtusifolia*. A. The tree extends roots around the palm; B. A cylinder of roots remains after the palm has died.

The development of *Cecropia* on *Phytelephas* seems to be different from that of hemiepiphytic species of *Ficus* that grow on palms. In the latter, the tree seeds germinate on the palm and the new plant produces roots that encircle the palm stem while growing geotropically; eventually, the fig becomes rooted in the ground (Smith 1956, Davis 1970, Putz & Holbrook 1989). Although fig roots also grow apogeotropically into the palm crowns (Putz & Holbrook 1989), these roots usually do not encircle the palm. Putz & Holbrook (1986) point out that hemiepiphytic stranglers on palms and other monocotyledons that lack secondary growth do not seem to cause much damage to the hosts, and explain the occasional cases of palm deaths as the effects of shading and root competition. In *P. seemannii*, on the contrary, the strangling *Cecropia* is rooted in the ground and its prop roots grow into the crown center. Strangulation takes place when the roots of *Cecropia* reach the center of the crown, and tighten around the young leaves and the spear leaves. Death is probably caused by compression of the petioles, impairing water and nutrient conduction to the new leaves (which explains leaf wilting and progressive reduction in size) and by the inability of the apical meristem to continue growth, due to lack of space. A palm may survive the "attack" of a *Cecropia* if its stem can elongate faster than the strangler's roots advance into the center of the crown. If the roots end up encircling only the stem, the palm is not killed. If the palm crown can keep ahead of roots until the strangler senesces, it will probably survive. Because cecropias generally die standing (Alvarez-Buylla & Martínez-Ramos 1992) death of the tree will not result in the breaking of the palm. The place of initial penetration of the *Cecropia* roots into the epiphytic humus mass, and the age of the invading tree, are probably decisive for the palm.

It apparently takes several years for a *Cecropia* to strangle a *Phytelephas* palm. This can be inferred from the size of trees that had killed or seemed about to kill palms; in all cases trees larger than 18 cm in diameter. Applying a best-fit line to Alvarez-Buylla & Martínez-Ramos' (1992) gap-age--plant-size relationship for *Cecropia obtusifolia* in Los Tuxtlas, Mexico, trees 18 cm dbh correspond to gaps *c.* 10 years old. In our study, a palm that had been recently killed by a *Cecropia* 28 cm in diameter grew in an area that had been cleared for rice planting about 15 years prior to our observation, according to local informants. The oldest individuals of *Cecropia obtusifolia* in Los Tuxtlas grew in gaps 37 years old (Alvarez-Buylla & Martínez-Ramos 1992); thus probably most *Phytelephas* palms are killed between 10 and 37 years after gap formation.

The two palms killed in the transect and in the plots represent 0.32 % of all palms in the sample. Considering that evidence of a strangled palm, in the shape of a cylinder of roots (Fig. 3B), can remain for up to 27 years (i. e., from the strangling at the age of 10 until death at 37), 0.32 % can be considered a conservative estimate of the percentage of palms strangled in 27 years. Thus, the annual death rate of *Phytelephas* caused by *Cecropia* can be estimated as 0.0032 / 27, i. e., in the order of 1 per 10^4 individuals. Our field observations indicate that this figure is in the same order of magnitude as the death rate of palms due to all unexplained causes, and is, after river channel migration (Bernal, Ms), the most important cause of adult palm mortality. Strangling of adults as a consequence of gap formation contributes to the renewal of the palm stands, because it is in gaps that *Phytelephas* seedlings develop into juveniles.

Litter trapping is perhaps not the explanation of the growth form of *Phytelephas seemannii* but a favourable consequence of it (Bernal, pers. obs.). Litter trapping may be one of the reasons why such large palms reach such great densities in the forest understory. Strangulation by *Cecropia* probably acts as a selective force against this litter-trapping growth form.

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