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# DISTRIBUTION OF THE HEMIEPIPHYTE OREOPANAX CAPITATUS AT THE EDGE AND INTERIOR OF A MEXICAN LOWER MONTANE FOREST

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ABSTRACT. Distribution of the hemiepiphytic non-strangler tree *Oreopanax capitatus* was investigated in relation to forest edge in a lower montane forest of central Veracruz, Mexico. Seedlings of *O. capitatus* were present at both the edge and the interior of the forest; saplings and adults were found exclusively at the edge. Mean height above ground at which *O. capitatus* individuals were established on their host was 7.6 m. *O. capitatus* was present only on trees ≥30 cm dbh. The most common host species was *Liquidambar macrophylla,* although individuals were also observed on *Quercus germana, Clethra mexicana, Trema micrantha,* and *Meliosma alba.* Host preferences could not be determined from available data. The occurrence of saplings and adults of *O. capitatus* at the forest edge, along rivers and roads, and on abandoned buildings, indicates that *O. capitatus* requires more exposed sites to become a reproductive individual. Forest fragmentation and increasing edge extent may affect *O. capitatus* population structure and size-class distribution.

Distribución de la hemiepífita (*Oreopanax capitatus* Decne. & Planch, Araliaceae) en el borde y el interior de un bosque nublado en México.

RESUMEN. La distribución de *Oreopanax capitatus,* un árbol hemiepífito no-estrangulador, se investigó en el borde y el interior de un bosque de neblina en el centro de Veracruz, México. Los resultados indicaron que las plántulas de *O. capitatus* están presentes en el borde y el interior del bosque pero que los juveniles y adultos se encuentran exclusivamente en el borde del bosque. La altura media sobre el suelo a la cual *O. capitatus* se establece sobre sus hospederos es 7.6 m. *Oreopanax capitatus* se encontró sólo sobre árboles ≥30 cm dap. *Liquidambar macrophylla* es el árbol hospedero más común, aunque también se observaron individuos establecidos sobre *Quercus germana, Clethra mexicana, Trema micrantha,* y *Meliosma alba.* Sin embargo, a partir de los datos disponibles no se pudieron determinar preferencias hacia hospederos. La presencia de juveniles y adultos de *O. capitatus* en el borde del bosque, a lo largo de rios y caminos y sobre ruinas indica que requiere de sitios expuestos para alcanzar una etapa de madurez. La fragmentación del bosque y el incremento en la extensión de bordes podría afectar la estructura de la población de *O. capitatus* y la distribución de los tamaños de clase.

## INTRODUCTION

Woody hemiepiphytes, plants that establish as epiphytes and later send roots to the ground, are common in many tropical vegetation types (Todzia, 1986; Lawton & Putz, 1988; Putz & Holbrook, 1989; Clark & Clark, 1990; Daniels & Lawton, 1991). Ecological studies of hemiepiphytes have focused primarily on physiological adaptations associated with the epiphytic phase (Putz & Holbrook, 1986). Studies on photosynthetic patterns in hemiepiphytic members of *Clusia* and *Ficus* indicate the existance of mechanisms to withstand water deficits (e.g., CAM in the case of some *Clusia* spp.) (Tinoco & Vazquez-Yanes, 1983; Ting *et al.,* 1985, 1987). Seed germination and seedling establishment (Titus *et al.,* 1990), habitat and host preferences (Daniels & Lawton, 1991), and nutrient relations of several *Ficus* spp. have also been studied (Putz & Holbrook, 1989).

Hemiepiphytes apparently prefer some host species and establishment sites over others as a mean of avoiding the shaded understory, since the amount of light received at particular sites is an important determinant of hemiepiphyte establishment (Putz & Holbrook, 1986; Daniels & Lawton, 1991). Forest fragmentation increases canopy openness at the forest edge and lateral penetration of light into the remnant forest (Williams-Linera, 1990). Thus, the establishment of hemiepiphytes and the growth of hemiepiphyte seedlings already present may be affected when an edge is created.

The objectives of this study were: 1) to determine the distribution and relative abundance of *O. capitatus* as seedlings, saplings, and adults at the edge and in the interior of a lower montane forest; and 2) to determine host preferences, host diameter, and the height at which *O. capitatus* is established.

## STUDY AREA

In central Veracruz, Mexico, a continuous lower montane wet forest (Holdridge *et al.,* 1971) existed until the beginning of this century (Marchal & Palma, 1985). At present, this forest is reduced to patches surrounded by coffee plantations, pastures, old fields, and human settlements. The study was conducted at Rancho Guadalupe, a protected forest area, next to the Francisco Xavier Clavijero Botanical Garden, 2.5 km south of Xalapa on the road to Coatepec (19°30′N, 96°57′W), and in other forest patches close to the Xalapa-Coatepec road. This area (1,225 m) receives 1,514 mm of annual rainfall. Mean annual temperature is 17.9°C. The forest edge was created at least 40 years ago, and it has a distinctive group of edge species of woody plants <5 cm dbh (pers. obs.).

## Plant Material

Hemiepiphytes occur in at least 20 families of dicotyledonous plants, the most diverse of which are Moraceae, Clusiaceae, and Araliaceae. Many of the hemiepiphytic species in the Araliaceae inhabit wet montane forests where they become established as epiphytes on standing trees as well as on fallen logs (Putz & Holbrook, 1986). The neotropical genus *Oreopanax* (Araliaceae) has ca. 80 species, ten of which have been reported in Mexico (seven in the State of Veracruz). Growth forms include trees (e.g., *O. xalapensis* (H.B. & K.) Decne. & Planch.), trees seldom found as hemiepiphytes (e.g., *O. obtusifolius* L. O. Williams), and trees frequently found as hemiepiphytes (e.g., *O. liebmanni* Marchal) (Sosa, 1979).

*Oreopanax capitatus* occurs from Southeast Mexico to the Andes of Colombia and Peru, and in Cuba and Santo Domingo. This hemiepiphytic tree is frequently observed growing on trees along rivers, roads, old buildings and ruins, and forest edges in the coffee region of central Veracruz, Mexico. Although a non-strangler, *O. capitatus* can become a free-standing tree (pers. obs.).

## Methods

To estimate the distance into the forest at which an edge effect could be detected, forest structure was quantified along three randomly selected transects from the forest border to 60 m into the forest. The dbh (diameter at 1.3 m) and species of all trees ≥5 cm dbh were recorded for six 10 m × 10 m plots located along each transect. Woody vegetation <5 cm dbh but >2 m tall was similarly measured in twelve 5 m × 5 m plots along each transect. Data on density (individuals $ha^{-1}$) and basal area ($m^2$ $ha^{-1}$) were fitted in a post-hoc two-piecewise regression model in order to estimate a breakpoint for these data, i.e., distance into the forest up to which edge effect was manifested on vegetation structure (Williams-Linera, 1990).

Spatial distribution of *O. capitatus* was determined in an area of 120 m × 60 m (long axis parallel to forest boundary), subdivided in 72 plots measuring 10 m × 10 m. In each plot, the presence of seedlings, saplings, or adults of *O. capitatus,* host trees species, and dbh were recorded. Seedlings were epiphytic plants <1 m tall; saplings (non-mature plants >1 m tall) and adults (mature plants) were individuals that had permanent roots reaching the ground. The height on the host tree at which individuals of *O. capitatus* apparently were established was measured with a rangefinder (when possible) or estimated. All observations were made using binoculars. Sampling was carried out in February (winter), when a portion of the canopy was leafless, which facilitated observation of epiphytes.

## Results and Discussion

Density and basal area of trees <5 cm dbh decreased with distance into the forest. When these data were fitted into the nonlinear regression model, the edge effect was estimated as occurring up to 18.5 m (standard error of the mean, SEM = 5.45) for basal area, and up to 13.9 m (SEM = 2.28) for density. The forest edge was thus considered to extend 20 m into the forest, and the remaining area sampled (20 to 60 m distance into the forest) was considered to be forest interior.

Seedlings of *O. capitatus* were present in the forest edge and interior, but saplings and adults were found exclusively at the edge. Within the entire area sampled, *O. capitatus* density was 20.8 individuals $ha^{-1}$, hemiepiphytic (saplings and adults) individuals density was 6.9 individuals $ha^{-1}$, and epiphytic (seedlings) density was 13.9 individuals $ha^{-1}$. At the forest edge, hemiepiphytic individuals were present at a high density (20.8 individuals $ha^{-1}$), but there were no individuals in the forest interior. In contrast, epiphytic individuals had a higher density in the forest interior (16.7 individuals $ha^{-1}$) than at the forest edge (8.3 individuals $ha^{-1}$). The density of *O. capitatus* was very high in comparison to hemiepiphyte density reported for forest on Barro Colorado Island (11.1 individuals $ha^{-1}$ for all hemiepiphytic species, and 0.3 individuals $ha^{-1}$ for *O. capitatus* only) (Todzia, 1986). Nevertheless, *O. capitatus* density was low when compared to the density of *Ficus* spp. in a palm savanna (Putz & Holbrook, 1989).

*Oreopanax capitatus* established at a mean height of 7.6 m (SEM = 1.1). *O. capitatus* individuals were found only on trees ≥30 cm dbh

TABLE 1. *Oreopanax capitatus* growth stage, height at which *O. capitatus* was established on the host trees, host tree species, and host tree dbh, in six strips (120 m × 10 m) parallel to the forest edge, from 0 to 60 m into the forest.

| Distance into the forest (m) | *O. capitatus* growth stage | Height on host (m) | | Host tree species | dbh (cm) |
|---|---|---|---|---|---|
| 0–10 | Adult | 4.5 | | *Liquidambar macrophylla* | 103 |
| | Juvenile | 10.0 | | *Meliosma alba* | 75 |
| | Seedling | 6.0 | | *Quercus germana* | 50 |
| 10–20 | Adult | 3.0 | | *Clethra mexicana* | 69 |
| | Adult | 5.9 | | *Liquidambar macrophylla* | 114 |
| | Juvenile | 3.5 | | *Liquidambar macrophylla* | 123 |
| | Seedling | 4.0 | | *Liquidambar macrophylla* | 37 |
| 20–30 | Seedling | 5.5 | * | *Liquidambar macrophylla* | 75 |
| | Seedling | | * | | |
| 30–40 | Seedling | 5.5 | | *Quercus germana* | 30 |
| 40–50 | Seedling | 17.0 | | *Quercus germana* | 84 |
| 50–60 | Seedling | 9.0 | * | *Clethra mexicana* | 56 |
| | Seedling | 12.8 | * | *Trema micrantha* | 76 |
| | Seedling | 7.0 | * | | |
| | Seedling | 15.0 | * | | |

* *O. capitatus* on same host tree.

(TABLE 1), possibly because trees <30 cm dbh present little colonizable surface. They were observed growing on five host tree species, including four co-dominant primary species, and one shade intolerant species (*Trema micrantha* (L.) Blume). They were most frequently observed on *Liquidambar macrophylla* even though this was the second most common species ≥30 cm dbh. No relationship was found between *O. capitatus* on *Liquidambar* versus non-*Liquidambar* trees ≥30 cm dbh (chi-square = 1.56, 1 df, $P > 0.05$). At the forest edge, both the density of trees ≥30 cm dbh and of *O. capitatus* was twice that of the forest interior, but density of trees ≥30 cm dbh and *O. capitatus* density were independent (chi-square = 2.7, 1 df, $P > 0.05$).

These results indicate that the apparent host preference of *O. capitatus* for *L. macrophylla* is a reflection of the abundance of trees ≥30 cm dbh. These results suggest that *O. capitatus* is a promiscuous epiphyte with regard to host preference. Clark and Clark (1990) report that in the lowland tropical wet forest at La Selva, Costa Rica, trees <30 cm dbh do not have hemiepiphytes and that liana and hemiepiphyte loads increase with host diameter. In the lower montane cloud forest of Monteverde, Costa Rica, host trees of *Ficus crassiuscula* ranged in dbh from 20 to 150 cm, but in contrast to *O. capitatus, F. crassiuscula* was not randomly distributed among host-tree species, it was more abundant on some host species than expected (Lawton, 1986; Daniels & Lawton, 1991). In the present study, a pioneer tree, *Trema micrantha,* supported three *O. capitatus* seedlings, although no other pioneer trees with dbh ≥10 cm were recorded in the study site. In contrast, pioneer trees (*Cecropia insignis* Liebm. and *C. obtusifolia* Bertol.) at La Selva lack hemiepiphytes (Clark & Clark, 1990).

*Oreopanax capitatus* seeds are probably dispersed by birds, as are several other Araliaceae species (Wheelwright et al., 1984). The presence of seedlings throughout the forest may reflect their ability to germinate under low light conditions. However, *O. capitatus* may need certain light conditions to reach the adult stage. *O. capitatus* trees appear to not compete for light with their hosts, since all the adults in the study area had their foliage under the host canopy (pers. obs.). Clark and Clark (1990) also report the impression that hemiepiphyte leaves were frequently borne deeper in the host's crown and were thus not strong competitors for leaf display space of the host trees. In contrast, F. E. Putz (pers. comm.) considers that some hemiepiphytes display their foliage above that of their hosts and thus may shade the host foliage. Canopy openness is higher at the forest edge than in the forest interior (Williams-Linera, 1990). The occurrence of adults of *O. capitatus* only at the forest edge (along roads and rivers, and on abandoned buildings) indicates that they require more exposed sites to reach a mature stage.

The occupancy of trees by *O. capitatus,* was apparently determined by host tree diameter class and abundance; host preferences could not be determined from the data at hand because of the small sample size. The size-class distribution of *O. capitatus* at the edge and interior of the forest may be related to the edge age. The adults recorded were initially established (or were present as seedlings) when the edge was created. Habitat fragmentation and increasing edge extent may have an impact on *O. capitatus* population structure. In order to test this assumption, experiments must be carried out on seed dispersion, seed germination and establishment, and seedling and adult physiological requirements.

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