NOTES ON THE FLORAL BIOLOGY OF *COUROUPITA GUIANENSIS* AUBL. (LECYTHIDACEAE)[1]

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Floral biology has been studied in relatively few Lecythidaceae, despite their ecological importance in the Neotropics. Only a few authors have dealt with the subject, notably Jackson and Salas (1965) on *Lecythis ellipitica* H.B.K., Dias (1967) on *Bertholletia excelsa* Humb. & Bonpl., Mori and Kallunki (1976) on *Gustavia superba* (Kunth) Berg., Prance (1983) on *Eschweilera garagarae* Pittier, and Prance (1976) and Mori et al. (1978) on pollination and androecial structure in the family as a whole. Ormond et al. (1981) published a contribution to the floral biology of *Couroupita guianensis* after all of our field observations were completed and a draft of this paper was submitted for publication. Prance (1976) and Mori et al. (1978) pointed out that the androecial zygomorphy and the position of the hood (adpressed to the ring) in *Couroupita subsessilis* Pilg. suggest that the genus *Couroupita* may be intermediate in the family with respect to androecial evolution. Few studies of anthesis behavior in tropical plants, including Lecythidaceae, have been carried out. Notably, Mori et al. (1978) reported diurnal anthesis and shedding of stamens during the late afternoon for *Lecythis amara* Aublet (= *L. alba* Mori, nom. nud.), and asynchronous anthesis during the morning for *Eschweilera longipes* (Poit.) Miers.; the latter of which sheds its androecia the following day. Differential behavior between pollen produced in ring anthers and that found in hood anthers is documented by Mori and Orchard (1979), Mori et al. (1980a), and Ormond et al. (1981). Floral visits by potential pollinators, such as wasps and small bees, have been reported by Prance (1976), Mori et al. (1978), and Ormond et al. (1981).

METHODS AND RESULTS

Cultivated individuals of *Couroupita guianensis* Aubl. were studied at the Jardin Botanico in Caracas, Venezuela, located near the limit of natural distribution of the species. Observations were recorded during two days in November 1979, and again for four days in June 1980, although the observed individuals flower throughout the year.

The flowers of *Couroupita guianensis* are very fragrant and attract many insect visitors. The petals are yellow both on the exterior and the interior, with rose to red-rose margins. The androecial column and filaments of the hood stamens are lilac, with the tip of the anthers yellow and the ring stamens white. A small amount of sticky secretion is present on the stigma. Anthesis is diurnal and asynchronic, the flowers beginning to open gradually between 7:00 and 8:30 A.M., with a peak around 8:00 A.M. (Fig. 1). The ring anthers open simultaneously with those on the hood, shortly after anthesis, but they retain pollen longer during the day (Fig. 2). The number of open flowers presenting pollen reaches a peak around 9:00 A.M.

Pollen in *Couroupita* is dimorphic; grains produced by anthers in the hood are released in tetrads and as such are clearly larger than the simple grains produced in the ring anthers. Furthermore, the hood anthers themselves are larger, containing an average of 2,850 tetrads, as compared with approximately 450 grains per ring anther. Tests for pollen viability show no germination of hood pollen in sacharose, as previously reported by Mori et al. (1980b) and by Ormond et al. (1981). However, Thompson (1921) reported that hood pollen was as fertile as ring pollen. Hood pollen stained well using cotton blue in lactophenol and it is reported by Ormond et al. (1981) as having significant protoplasm in 88% of pollen grains tested using aceto carmine. These reports raise doubts as to the reliability of both staining methods for assessing pollen viability.

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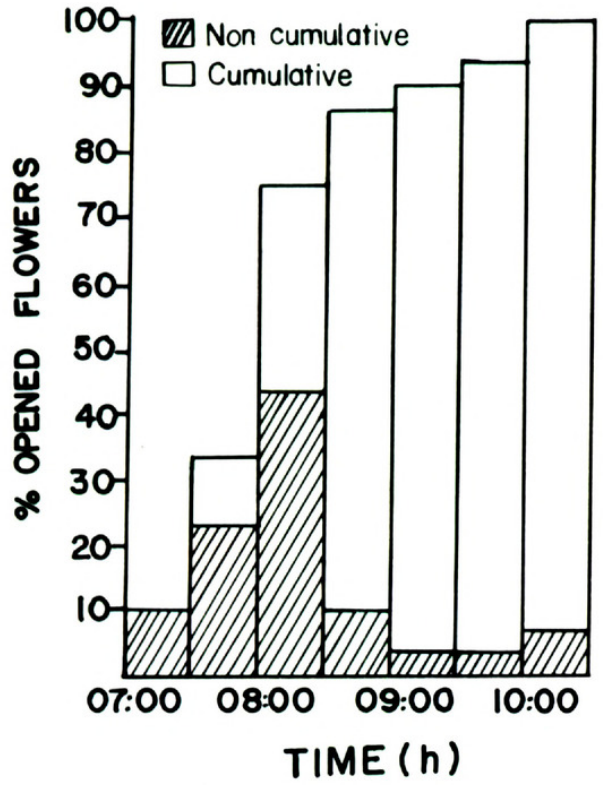

FIGURE 1. Anthesis behavior in *Couroupita guianensis.*

Insects captured visiting flowers were bees belonging to *Apis mellifera, Bombus* sp., *Trygona* sp., and *Xylocopa frontalis* (Oliver), the wasp *Polybia,* and the flower fly *Ornidia obesa* F. (Diptera, Syrphidae). More frequent visits were made by the larger insects, such as individuals of the bee genera *Bombus* and *Xylocopa,* which have been reported as visitors to Lecythidaceae, including species of *Gustavia, Eschweilera, Couratari,* and *Couroupita guianensis.* Less frequent visits were made by the smaller insects, such as

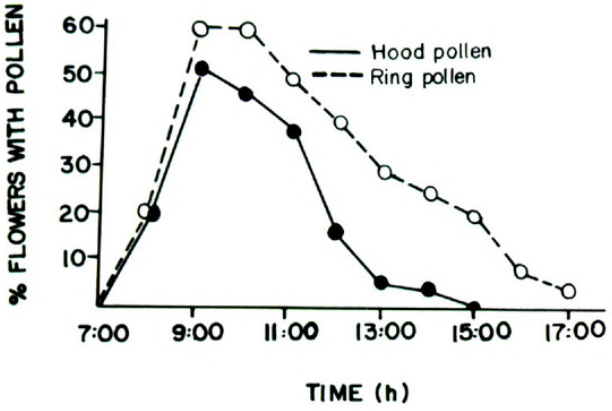

FIGURE 2. Comparison of behavior of anther dehiscence and pollen extinction between the hood and the ring in flowers of *Couroupita guianensis.*

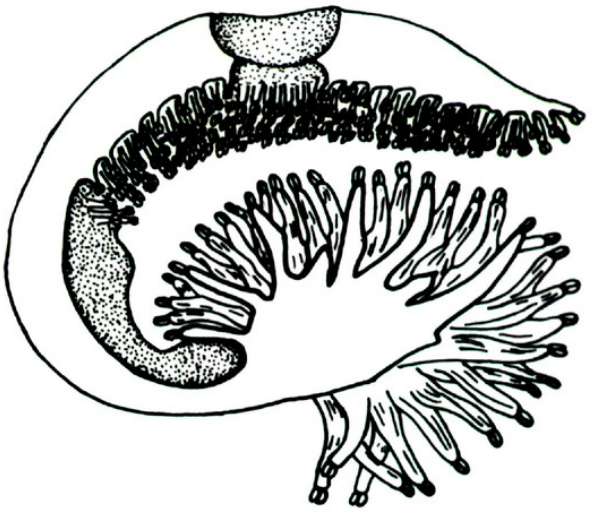

FIGURE 3. Medial schematic section of androecium in *Couroupita guianensis.*

species of *Apis, Trigona,* and the wasp genus *Polybia,* which have been observed in numerous Lecythidaceae, including *Couroupita subsessilis,* a species which has much smaller flowers (Prance, 1976). Thus, *Couroupita guianensis* differs from *C. subsessilis,* as well as other Lecythidaceae, in atracting both small and larger insects, including species of the mentioned genera.

The hood anthers of *C. guianensis* provide a convenient landing platform for these floral visitors, because the flowers are inverted and hanging (Fig. 3). The open structure of the androecium facilitates access to insects of various sizes. While collecting hood pollen, larger bees rub their dorsal areas against the ring anthers and the stigma, detaching several ring anthers in the process. This behavior assures transfer of ring pollen to the stigma. Apparently hood pollen may also reach the stigma, however, because insects were observed to turn over completely within the flower. Individuals of *Trigona* forage for pollen

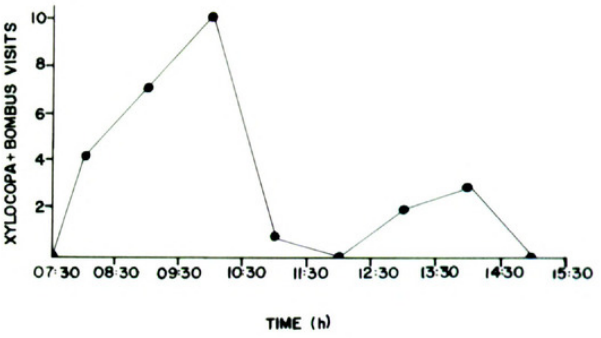

FIGURE 4. *Bombus* and *Xilocopa* visits recorded, as an average of five days, in flowers of *Couroupita guianensis.*

on ring anthers during long periods, probably affecting pollination, whereas other small floral visitors wander throughout the flower in such a manner that only their ventral surfaces contact the anthers, and pollination thus occurs only accidentally.

Data on frequency of floral visits by individuals of *Bombus* sp. and *Xylocopa frontalis* were recorded (Fig. 4). Visits began at anthesis and continued throughout the day, with peaks occurring around 10:00 A.M. and 2:00 P.M., and a drop to near zero and around noon. *Bombus* species tended to visit predominantly in the morning, while *Xylocopa* were more common in the early afternoon.

Discussion

Our findings on pollen fertility and pollen behavior confirm that pollination is achieved only with ring pollen. However, hood pollen, which should be rich in nutrients, as suggested by its living protoplasm, provides only food for the pollinators, and plays an important role in the process of pollination, as was previously stated by Ormond et al. (1981).

Our observations for *Couroupita guianensis* as compared to reported data for *C. subsessilis* (Prance, 1976) suggest that differential use of pollinators may be important in the evolution and maintenance of species within the genus. It is interesting to note that individuals of *Bombus* and *Xylocopa* have been seen on putatively primitive Lecythidaceae such as *Gustavia,* as well as on more advanced taxa such as species of *Couratari.* It is therefore not surprising to find these larger floral visitors on *Couroupita,* whose androecial structure is apparently intermediate within the family.

The asynchronous behavior of anthesis observed in *C. guianensis* may tend to compensate for the short life of the flowers of this species and could be viewed as a way to promote cross pollination by means of prolonging pollen presentation for a period of nearly two hours. This hypothesis is supported by the distribution of visits by insects: most visits were recorded during morning hours, at a time when a maximum number of anthers is open.

The recorded frequency of floral visits, which shows that *Bombus* species tend to visit predominantly in the morning whereas *Xylocopa* were more common in the early afternoon, may document a case of temporal resource partitioning by the insects to reduce competition for pollen.

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