Extrafloral Nectaries: Their Taxonomic Distribution and Abundance in the Woody Flora of Cerrado Vegetation in Southeast Brazil[1]

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ABSTRACT

The taxonomic distribution and abundance of woody plants with extrafloral nectaries (EFNs) are reported for different areas of cerrado vegetation (subtropical savanna) in the state of São Paulo, southeast Brazil. Thirty-four plant species belonging to 15 families were found to have EFNs. The Mimosaceae (6 species) and Bignoniaceae and Vochysiaceae (4 species each) were the families most frequently bearing EFNs. Glands associated with vegetative parts (leaves, stem) were more common (91.2%) than those found near the bud or flower (20.6%). The percentage of EFN-bearing species within the woody floras of 5 cerrado areas in São Paulo ranged from 15.5 to 20.2. The abundance of plants with EFNs in these areas varied from 7.6 to 20.3 percent. These results are compared with data obtained from other similar studies undertaken in temperate and tropical habitats.

RESUMO

A distribuição taxonômica e abundância de plantas lenhosas com nectários extraflorais (NEFs) são registradas para diferentes áreas de vegetação de cerrado do estado de São Paulo, no sudeste do Brasil. NEFs foram encontrados em 34 espécies pertencentes a 15 famílias. As Mimosaceae (6 espécies) e Bignoniaceae e Vochysiaceae (4 espécies cada) foram as famílias portadoras de NEFs mais representativas. Glândulas associadas a partes vegetativas (folhas, ramo) foram mais comuns (91.2%) do que aquelas encontradas próximo ao botão ou flor (20.6%). A porcentagem de espécies lenhosas com NEFs em 5 áreas de cerrado de São Paulo variou de 15.4–20.2. A abundância de plantas com NEFs nestas áreas variou de 7.6–20.3 porcento. Estes resultados são comparados com dados obtidos em outros estudos similares realizados em áreas temperadas e tropicais.

PLANTS BEARING EXTRAFLORAL NECTARIES (EFNs) have attracted the attention of naturalists for more than a century. The immense structural variability of EFNs and their widespread occurrence in many plant taxa have been evidenced by the reviews of several authors (*e.g.,* Zimmermann 1932; Schnell *et al.* 1963; Bhattacharyya & Maheshwari 1971a, b; Bentley 1977a; Elias 1983). Moreover, the relevance of EFNs as useful taxonomic characters has been stressed by Siebert (1948), Bhattacharyya and Maheshwari (1971a, b), and Keeler and Kaul (1979). The adaptive significance of EFNs has been a controversial topic since their discovery by early botanists (see Bentley 1977a and citations within). Recent studies have shown that, in general, the ecological function of EFNs is to attract insects, particularly ants, that protect the plant against herbivores (Elias & Gelband 1975; Bentley 1977a, b; Keeler 1977, 1980a, 1981a; Tilman 1978; Inouye & Taylor 1979; Schemske 1980), but in some cases the adaptive nature of EFNs is still not well understood (*e.g.,* Tempel 1983, Heads & Lawton 1984, Lawton & Heads 1984). Little is known about the taxonomic distribution and abundance of EFN-bearing plants in different vegetation types, especially in South America. Data of this kind are reported for the first time for woody plants in cerrado vegetation in Brazil.

METHODS

Field work was done during 1983 and 1984 in different areas of cerrado *sensu strictu* (Goodland 1971) of the state of São Paulo in southeastern Brazil (Fig. 1). Data on the taxonomic distribution and abundance of woody plants with EFNs were based on floristic surveys conducted jointly by H. F. Leitão Filho and colleagues of our cerrado study group, or during field courses sponsored by our Graduate Program in Ecology. Only trees and shrubs with a basal trunk diameter of at least 3 cm were included in these surveys, and the sampling methods applied for different cerrado areas were 20 quadrats of 10 × 25 m each in São Simão and Moji-Mirim, 25 quadrats of 10 × 25 m each in Itirapina and Luís Antonio, and 60 quadrats of 10 × 25 m in Mogi-Guaçu. All plant species registered

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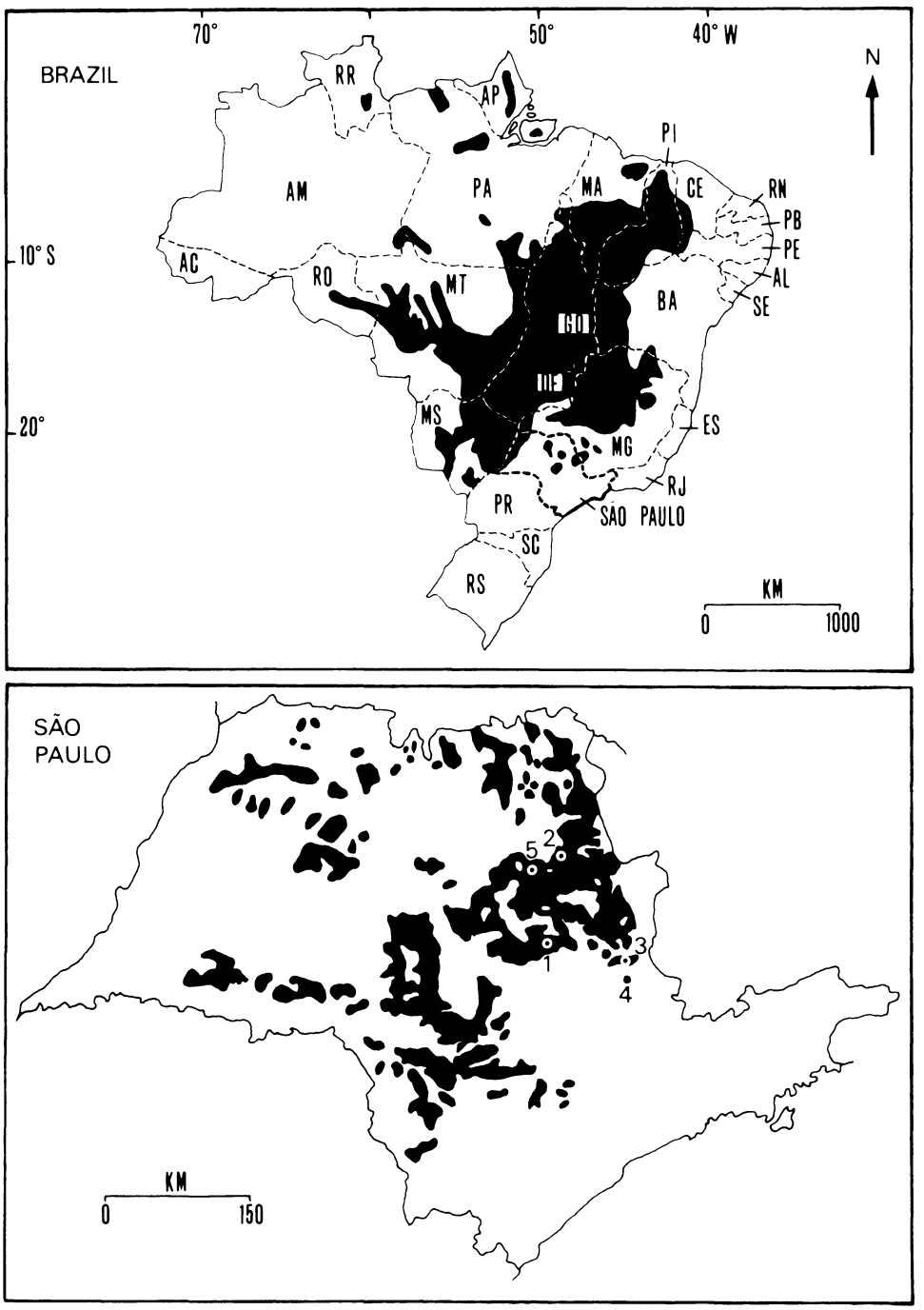

FIGURE 1. Maps showing the distribution of cerrado vegetation (dark area) in Brazil and in the state of São Paulo (after Borgonovi and Chiarini, 1965). Numbers in the inset map of São Paulo refer to cerrado sites (small circles) where surveys have been conducted: (1) Itirapina, (2) São Simão, (3) Mogi-Guaçu, (4) Moji-Mirim, (5) Luís Antonio.

TABLE 1. *Woody plant species bearing extrafloral nectaries in cerrado vegetation, São Paulo, Brazil.*

Plant species	Site of nectary	Type of nectary[a]
Bignoniaceae		
Arrabidaea brachipoda (DC.) Bur.	leaf blade	flattened
Cybistax antisyphillitica Mart.	leaf blade	flattened
Tabebuia caraiba (Mart.) Bur.	leaf blade	flattened
Tabebuia ochracea (Cham.) Standl.	leaf blade	flattened
Bombacaceae		
Eriotheca gracilipes (Schum.) Robyns	petiole	flattened
Caesalpinaceae		
Bauhinia rufa (Bong.) Steud.	intrastipular trichomes	scalelike
Cassia rugosa D. Don.	rachis	elevated
Cassia speciosa Schrad.	rachis	elevated
Caryocaraceae		
Caryocar brasiliense Camb.	calyx	flattened
Chrysobalanaceae		
Licania humilis Cham. & Schl.	leaf blade	flattened
Combretaceae		
Terminalia argentea Mart. & Zucc.	petiole	elevated
Terminalia brasiliensis Camb.	petiole	elevated
Lythraceae		
Lafoensia paccari St. Hil.	leaf blade	elevated
Malpighiaceae		
Heteropteris acutifolia Juss.	leaf blade	elevated
Heteropteris byrsonimifolia Juss.	leaf blade	elevated
Mimosaceae		
Anadenanthera falcata (Bent.) Speg.	rachis	elevated
Enterolobium gummiferum (Mart.) Macbr.	rachis	elevated
Plathymenia reticulata Benth.	stem	elevated
Stryphnodendron adstringens (Mart.) Cov.	rachis	elevated
Stryphnodendron obovatum Benth.	rachis	elevated
Stryphnodendron polyphyllum Mart.	rachis	elevated
Myrsinaceae		
Rapanea guianensis Aubl.	leaf blade	scalelike
Rapanea lancifolia Mez.	leaf blade	scalelike
Ochnaceae		
Ouratea castanaefolia (DC.) Engl.	cataphylls	flattened
Ouratea spectabilis (Mart.) Engl.	cataphylls	flattened
Rosaceae		
Prunus sellowii Koehne	leaf blade	flattened
Rubiaceae		
Tocoyena brasiliensis Mart.	calyx	elevated
Tocoyena formosa (C. & S.) K. Schum.	calyx	elevated
Verbenaceae		
Aegiphila lhotzkiana Cham.	leaf blade	flattened
Aegiphila sellowiana Cham.	leaf blade	flattened
Vochysiaceae		
Qualea dichotoma (Mart.) Warm.	stem, pedicel	elevated
Qualea grandiflora Mart.	stem, pedicel	elevated
Qualea multiflora Mart.	stem, pedicel	elevated
Qualea parviflora Mart.	stem, pedicel	elevated

[a] According to Elias (1983), after Zimmermann (1932): "Flachnektarien" = flattened nectaries; "Hochnektarien" = elevated nectaries; "Schuppennektarien" = scalelike nectaries.

in these surveys, including those found out of the sampled areas, were searched in the field for EFNs. Evidence for the presence of EFNs was obtained *a priori* from published lists of species bearing such glands (Schnell *et al.* 1963, Bentley 1977a, Elias 1983). An EFN was considered present if nectar was secreted, whether or not a differentiated structure was detected. The observation of stereotypical nectar-gathering behavior by ants or other nectar feeders, although not used as a criterion, occasionally served as a cue for detecting the presence and location of EFNs. When necessary, anatomical sections were made to investigate the nature of nectar-secreting structures. We have adopted Delpino's (1875) functional system of defining nectaries, regarding as extrafloral those nectaries not directly involved with pollination functions (even if the gland is associated with the reproductive parts of a plant). Plant taxonomy follows Cronquist (1981), and voucher specimens are deposited in the herbarium of the Universidade Estadual de Campinas (UEC).

THE CERRADO VEGETATION

The cerrados embrace an area of 2 million km^2, which corresponds approximately to 25 percent of the Brazilian territory (Ferri 1977). Their geographical distribution includes large parts of the states of Mato Grosso (MT), Mato Grosso do Sul (MS), Goiás (GO), Distrito Federal (DF), Minas Gerais (MG), Maranhão (MA), and Piauí (PI) (Fig. 1). Within their distribution the cerrados present several intergrading physiognomic forms, of which Goodland (1971) recognized 4 main structural types: forest with more or less merging canopy (*cerradão*), dense scrub of shrubs-trees (*cerrado, sensu strictu*), open scrub (*campo cerrado*), and open grassland with scattered shrubs (*campo sujo*). Floristic studies of cerrados began with Warming (1908), but the most thorough surveys are those of Rizzini (1963), Eiten (1972), and Heringer *et al.* (1977). According to these authors the Brazilian cerrados contain approximately 780 species of trees and shrubs; the Fabaceae, Caesalpinaceae, Mimosaceae, Malpighiaceae, Vochysiaceae, Myrtaceae, and Melastomataceae being the most representative families, in number of both species and individuals.

The state of São Paulo is situated at the southern limit of the cerrado (Fig. 1), which here occurs in isolated patches corresponding to nearly 8 percent of the state's physical area. Several floristic surveys of the cerrado in São Paulo have been conducted recently (Giannotti & Leitão Filho 1979, Gibbs *et al.* 1983, Mantovani 1983, Toledo Filho 1984). These surveys show that the woody component of the cerrado vegetation of São Paulo contains most of the species recorded for the nuclear area of the cerrado distribution, although a few species more characteristic of neighboring semideciduous forests also occur in the cerrados of São Paulo. As a whole the woody component is less diversified in São Paulo than in the nucleus of the cerrado domain and includes approximately 150 species of trees and shrubs.

RESULTS AND DISCUSSION

The taxonomic distribution of plants with EFNs within cerrado woody species, as well as the location on the plant and the type of glands, is summarized in Table 1. A total of 34 plant species belonging to 15 families were found to have EFNs. The families most often having EFNs are the Mimosaceae (6 species) and Bignoniaceae and Vochysiaceae (4 species each). These are usually among the most common families in the cerrados of São Paulo and may together account for more than 15 percent of the individuals (*cf.* Table 2 for the Mogi-Guaçu area). The list in Table 1 adds some new occurrences in specific and generic categories to the EFN-bearing families cited by Elias (1983); we also report (probably for the first time) the Myrsinaceae as a family having EFNs, here represented by the genus *Rapanea* (Fig. 2i, j, k).

The locations of EFNs on the plants vary (Table 1, Figs. 2–4). Glands associated with vegetative parts (*e.g.,* leaves, stem) are more common (31 of 34, 91.2%) than those found near the bud or flower (7 of 34, 20.6%) ($\chi^2 = 15.16$; $P < 0.001$). The most common location is on the leaf blade (13 of 34, 38.2%), distributed among 7 different families (Table 1, Fig. 2). Nectaries on the rachis and on the stem occurred, respectively, on 20.6 percent (7 of 34) and 14.7 percent (5 of 34) of the plant species; the former are exclusive to legume genera (Fig. 4), and the latter are observed mainly in *Qualea* (Fig. 3f), a genus in the Vochysiaceae which also has glands on the pedicels. Elias (1983) mentions that nectaries on the inner surface of the sepals are present in all members of the Vochysiaceae, but as such glands in *Qualea* could reward pollinating bees, they are not regarded as extrafloral in this study. EFNs on the outer surface of the calyx were observed in *Caryocar brasiliense* (bat-pollinated; see Vogel 1968, Gribel 1984) and *Tocoyena brasiliensis* and *T. formosa* (moth-pollinated; see Silberbauer-Gottsberger 1972), whose buds are commonly occupied by ants (Fig. 3g, h).

Elevated and flattened nectaries were the most common types of nectaries found, occurring respectively on 19 and 12 species ($\chi^2 = 1.58$; $0.20 < P < 0.30$; n.s.). Scalelike nectaries were present only on 3 species. Elevated nectaries usually produced more nectar than the other types, and nectar-feeding insects (particularly ants) were more frequently observed visiting EFNs within this structural category (*e.g.,* Fig. 4).

Table 3 shows the proportion and abundance of EFN-bearing species within the woody floras of 5 cerrado areas in the state of São Paulo. The percentage of woody species with EFNs in these areas ranged from 15.4 to 20.2 per-

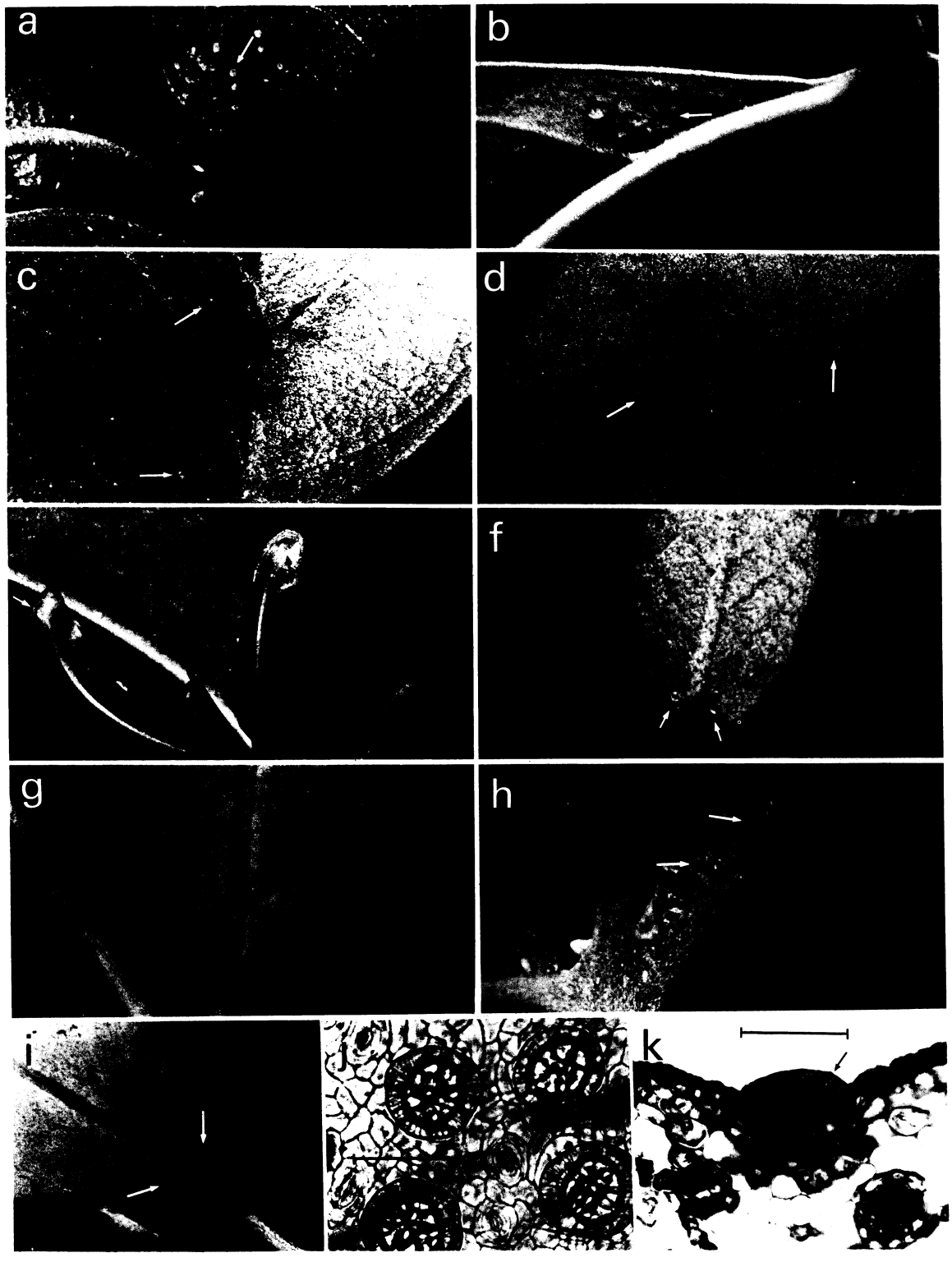

FIGURE 2. Plant species with extrafloral nectaries (arrows) on the leaf blade. a. *Arrabidaea brachipoda* (ant visitor is *Camponotus crassus*). b. *Cybistax antisyphillitica*. c. *Tabebuia ochracea* (ant visitor is *Camponotus crassus*). d. *Licania humilis*. e. *Lafoensia paccari*.

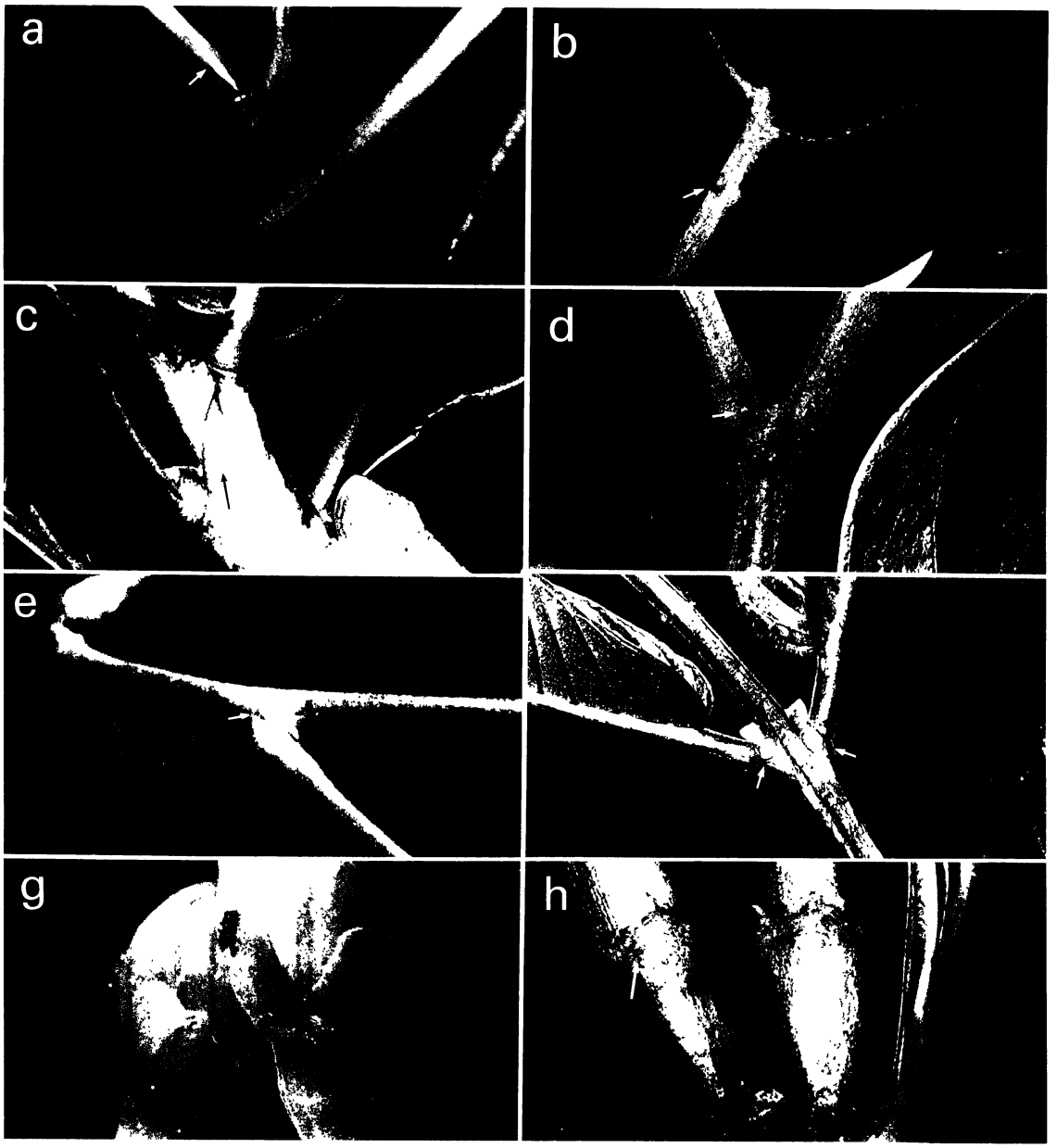

FIGURE 3. Plant species with extrafloral nectaries (arrows) on petiole (a, b), cataphyll (c), intrastipular trichome (d), stem (e, f), and calyx (g, h). a. *Eriotheca gracilipes*. b. *Terminalia argentea*. c. *Ouratea spectabilis*. d. *Bauhinia rufa*, note droplet on trichome (stipule fallen) and worker of *Camponotus*. e. *Plathymenia reticulata*. f. *Qualea grandiflora*. g. *Caryocar brasiliense* (ant visitor is *Crematogaster* sp.). h. *Tocoyena brasiliensis*.

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f. *Heteropteris byrsonimifolia*. g. *Prunus sellowii*. h. *Aegiphila lhotzkiana*. i. *Rapanea guianensis* (arrows indicate location of highest concentration of glandular trichomes). j. Four glandular trichomes (scalelike nectaries) of *Rapanea lancifolia* (scale bar = 0.11 mm). k. Longitudinal section of the leaf blade of *R. lancifolia* showing a glandular trichome. Scale bar = 0.13 mm.

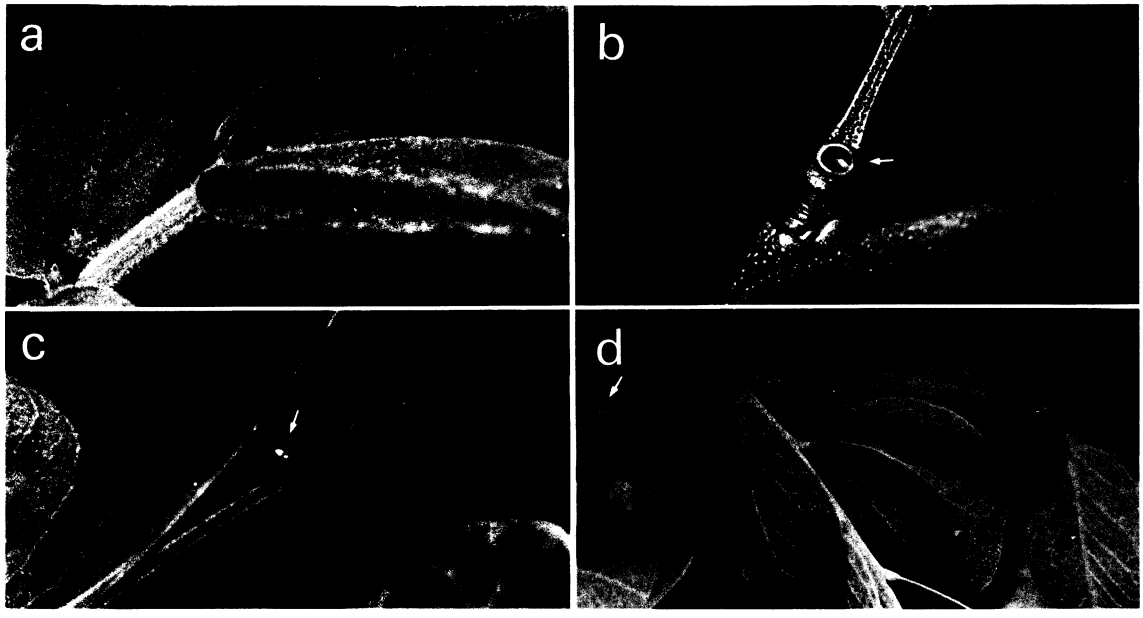

FIGURE 4. Legume species with extrafloral nectaries (arrows) on the rachis. a. *Cassia rugosa* (ant visitor is *Camponotus* sp.). b. *Anadenanthera falcata*. c. *Enterolobium gummiferum*, note droplet. d. *Stryphnodendron adstringens* (ant visitor is *Camponotus crassus*).

cent. We also have examined 194 of 774 species of trees and shrubs cited by Heringer *et al.* (1977) for the whole Brazilian cerrados: 17.5 percent (34 of 194) of the species examined have EFNs, a value which lies within the range found for São Paulo areas (Table 3). The cover of woody plants with EFNs in the cerrados of São Paulo varied from 7.6 to 20.3 percent ($\bar{x}$ = 15.8%). The low abundance of plants with EFNs in the cerrado of Luís Antonio (6.7%, see Table 3) was due to an atypically high frequency of 5 species without EFNs—*Copaifera langsdorfii, Dipty-chandra aurantiaca, Myrcia lingua, Pterodon pubescens,* and *Xylopia aromatica*—which account for 55.9 percent (1916 of 3428) of the woody plants sampled (*cf.* Toledo Filho 1984).

TABLE 2. *Occurrence and abundance of woody species within families bearing extrafloral nectaries (EFNs) in the cerrado vegetation of Mogi-Guaçu, São Paulo, Brazil.*

Families with EFNs sampled[a]	No. of species sampled[a]	No. of species with EFNs sampled[b]	Abundance of plants with EFNs in the family (%)	Abundance of the family in the whole flora (%)
Bignoniaceae	2	2	100 (490/490)	5.2
Bombacaceae	3	1	80.6 (54/67)	0.7
Caesalpinaceae	5	1	55.1 (91/165)	1.7
Caryocaraceae	1	1	100 (55/55)	0.6
Chrysobalanaceae	2	1	14.2 (20/141)	1.5
Combretaceae	1	1	100 (1/1)	0.0
Lythraceae	1	1	100 (7/7)	0.1
Malpighiaceae	4	1	3.7 (5/135)	1.4
Mimosaceae	3	3	100 (407/407)	4.3
Myrsinaceae	3	2	6.8 (13/191)	2.0
Ochnaceae	1	1	100 (177/177)	1.9
Rubiaceae	7	2	14.3 (10/70)	0.7
Verbenaceae	2	1	57.8 (11/19)	0.2
Vochysiaceae	5	3	96.5 (579/600)	6.4
Total	40	21	76.6 (1920/2525)	26.8 (2525/9435)

[a] Based on floristic survey from Gibbs *et al.* (1983); 60 quadrats of 10 × 25 m.
[b] See also Table 3.

TABLE 3. *Occurrence and abundance of woody species with extraflora nectaries (EFNs) in cerrado vegetation, São Paulo, Brazil.*

Area	Total no. of woody species[a,b]	Percentage with EFNs[b]	No. of species sampled[a,c]	Percentage with EFNs sampled	Percent cover of plants with EFNs
Itirapina	117	15.4 (18/117)	117	15.4	17.5 (879/5029)
São Simão	106	19.8 (21/106)	65	20.0	18.6 (426/2295)
Mogi-Guaçu	104	20.2 (21/104)	104	20.2	20.3 (1920/9435)
Moji-Mirim	144	16.7 (24/144)	103	16.5	15.1 (479/3167)
Luís Antonio	113	19.5 (22/113)	64	21.9	7.6 (262/3428)
Mean ± SD	116.8 ± 16.1	18.3 ± 2.1	90.6 ± 24.5	18.8 ± 2.7	15.8 ± 5.0

[a] Based on floristic surveys from: Giannotti and Leitão Filho, 1979 (Itirapina); UNICAMP's Graduate Program in Ecology (São Simão); Gibbs *et al.*, 1983 (Mogi-Guaçu); Toledo Filho *et al.*, 1984 (Moji-Mirim); Toledo Filho,1984 (Luís Antonio).
[b] Include species found out of the sampled area, except for Itirapina and Mogi-Guaçu.
[c] Quadrats of 10 × 25 m, see Methods.

Some rough comparisons with other studies undertaken in temperate and tropical habitats are pertinent for elucidating general geographical tendencies. Keeler (1979b) found in floristic surveys that the proportion of EFN-bearing dicotyledonous species in Nebraska is 3.8 percent; this value drops to 2.3 percent (28 of 1228) when only woody species are considered. Using quantitative sampling methods, Keeler (1980b, 1981b) also reported the mean cover of plants with EFNs as ranging from 0 to 14 percent in different habitat types in Nebraska and California. In tropical habitats, transect samples seem to indicate a quite different pattern: Bentley (1976) found that the cover of EFN-bearing plants ranged from 10 to 80 percent in tropical riparian and dry Costa Rican forest sites, and in Jamaica Keeler (1979a) reported this cover as 28 percent at sea level and 0 percent at 1310 m. If the values we have obtained for the woody flora of the cerrado (Table 3) are as high as (*i.e.*, comparable with) those related above, then Bentley's (1977a) and Gilbert's (quoted in Orians 1974) assertion that EFNs are more common in tropical than temperate environments seems valid.

The study conducted by Morais (1980) in the cerrado of Mogi-Guaçu on the arboreal ant community enhances the importance of woody plants for this insect guild. The stem-nesting subguild comprised 27 species, and the ground-nesting one contained 13 species; 2 species nested in either substrate. Plants with EFNs comprised 41 percent (56 of 136) of the live woody plants found to house ant colonies within 1075 m^2 of the cerrado (Morais, 1980). The ecological significance of the interactions between nectar-feeding insects, particularly ants, and EFN-bearing woody plants has never been investigated in cerrado vegetation. We intend to concentrate future studies on the nature of these interactions, hoping that this approach will cast further light on the relevance of EFNs for the cerrado community.

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