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Review article

Important bee plants for stingless bees (*Melipona* and Trigonini) and Africanized honeybees (*Apis mellifera*) in neotropical habitats: a review

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Summary — This paper reports on pollen and nectar sources for stingless bees in neotropical habitats. Some 288 species were considered important bee plants. Eighty of these were important for the Africanized honeybee. Plant families with the largest number of important species for both bee groups are also among those with the greatest diversity in neotropical regions. Some differences among the bee groups are highlighted

Africanized honeybee / *Melipona* / Trigonini / bee plant / neotropics

INTRODUCTION

Studies of flower visiting by species of stingless bees and Africanized honeybees in neotropical regions of the Americas are still few and far between, and limited in scope, with variable objectives and methodologies (Absy and Kerr, 1977; Roubik, 1978, 1979; Iwama and Melhem, 1979; Absy *et al,* 1980, 1984; Engel and Dingemans-Bakels, 1980; Sommeijer *et al,* 1983; Imperatriz-Fonseca *et al,* 1984, 1987, 1989; Silveira *et al,* 1984; Ramalho *et al,* 1985, 1989; Roubik *et al,* 1986; Kleinert-Giovannini and Imperatriz-Fonseca, 1987; Kleinert-Giovannini *et al,* 1987; Cortopassi-Laurino and Ramalho, 1988; Ramalho, 1990). Thus any review such as this must be selective and preliminary in nature. Bee plants have been characterized most frequently in relation to observations of Africanized and European honeybees when visiting flowers, and this has yielded significant information on bee plants (Crane *et al,* 1984), but at the same time this makes comparison with other bee species difficult. As to studies of the floral origin of honey using pollen grains analysis (*eg* Barth, 1970 a,b), they present estimates of nectar collecting from each plant species, but these are subject to errors of interpretation due to variations between different plant species in terms of pollen grains production. With a few exceptions, studies of bee communities (Sakagami *et al,* 1967; Sakagami and Laroca, 1971; Heithaus, 1979; Roubik, 1978, 1979; Cortopassi-Laurino, 1982; Laroca *et al,* 1982; Hakim, 1983; Opler, 1983; Orth, 1983; Camargo and Masukato, 1984; Knoll, 1985; Bortoli, 1987; Knoll *et al,* 1987; Almeida and Laroca, 1988; Knoll, 1990) fail to present data on the use of specific floral sources, since they deal with ecological questions at a different level of analysis, such as: diversity and phenology of bee species, characterization of syndromes and guilds of flower visitors, etc.

Hence in this review of bee plant species in neotropical zones, we have only considered quantitative information on flower visiting which permits a comparison of the value of specific floral sources for stingless bees and for Africanized honeybees. Most of the data used were based on melissopalynological studies, whose positive and negative aspects are notorious (Louveaux *et al,* 1978).

METHODS

The important floral sources of pollen and nectar for stingless bees (*Melipona* and Trigonini) and Africanized honeybees in neotropical habitats were reviewed and a synthesis prepared. The species important for Africanized honeybee were included in the results taken from studies comparing Africanized honeybee and stingless bees. With regard to the plant species already included in the list according to the above criterion, supplementary information taken from studies of Africanized honeybees was added.

Most the data were obtained *via* a pollen analysis of the food collected by bees. In these cases, we selected only plant species with a pollen representativity exceeding 10%, or from the pollen categories "frequent" (5–30%), "abundant" (> 30%), "secondary" (15–45%), and "predominant" (> 45%), in accordance with classification schemes used by various authors (Iwama and Melhem, 1979; Engel and Dingemans-Bakels, 1980; Sommeijer *et al,* 1983; Imperatriz-Fonseca *et al,* 1984, 1987, 1989; Ramalho *et al,* 1985, 1989; Kleinert-Giovannini and Imperatriz-Fonseca, 1987; Ramalho, 1987; Cortopassi-Laurino and Ramalho, 1988). Absy's studies (Absy and Kerr, 1977; Absy *et al,* 1980, 1984) provided us with the plant species most frequently found in pollen and nectar samples, those most persistent throughout the year (in number of months), or those visited by the largest number of stingless bees. Roubik *et al's* study (1986) provided us with references to the plant species "heavily" utilized by bees for pollen. A few field studies were used to list plant species visited by > 5% of the total number of individuals of some species of stingless bee and Africanized honeybee on flowers (Sakagami and Laroca, 1971; Orth, 1983; Knoll, 1985; Knoll and Imperatriz-Fonseca, 1987; Almeida and Laroca, 1988; Knoll, 1990).

RESULTS AND DISCUSSION

The data on flower visiting by species of stingless bees and Africanized honeybee (*Apis mellifera* L) in neotropical habitats are summarized in table I. Of the 23 studies mentioned, 5 compare Africanized honeybee and stingless bees, and a further 6 compare *Melipona* and Trigonini. In 6 of the studies, there is information on *Melipona* alone, and in 9 others, the information concerns only Trigonini. The data shown in table II are therefore biased as regards the number of plant species visited by the different groups of bees, or by 2 or more groups. The studies were conducted in areas with different types of vegetation, influenced in some cases by the presence of agriculture, pasture and or urbanization. Some studies were carried out in natural forests, a very few in grasslands or savannah. Herbaceous species and shrubbery, both ruderal and opportunistic, albeit originally under forest cover, are evidently abundant in areas with open vegetation.

Table II shows all the plant species with the highest levels of representativity in the diet of these bees in accordance with the quantitative studies listed in table I. Particularly in the case of the plant families of greatest significance for bees in neotropical zones, some common trends in latitudinal distribution may be detected. Generally speaking, the families with a larger number of species, *ie* Anacardiaceae, Compositae, Euphorbiaceae, Labiatae, Leguminosae, Melastomataceae, Moraceae, Myrtaceae, Palmae, Rubiaceae and Solanaceae, are also the most consistent pollen and nectar

Table I. Summarized data from quantitative studies on flower visiting by stingless bees and Africanized honeybees, in neotropical habitats.

Authors	*Bee species*	*Place/Vegetation*	*No and type of samples*					*Period*	*Bee*
			Stored pollen	*Stored honey*	*Pollen loads*	*Nectar loads*	*Field observations*	*(months)*	*plants**
1 Absy and Kerr (1977)	*Ms*	Manaus – Brazil / Amazon forest zone	–	–	267	–	–	12	06
2 Absy *et al* (1980)	*Ms*	Manaus – Brazil /	–	–	–	302	–	12	14
	Mr	Amazon forest zone	–	–	–	302	–	12	
3 Absy *et al* (1984)	*Fsi, Mfu, Mi, Mr, Mtu, Nm, Ot, Pl, Pm, Pp, Pv, Sp, Spl, Tam, Tc, Tch, Tfu, Tg, Tpa*	Amazon forest zone	37	–	–	–	–	02	13
4 Almeida and Laroca (1988)	*Ts*	Southern Brazil (review)	–	–	–	–	na	na	22
5 Arriaga (1989)	*Psp*	Chiapas – Mexico / Tropical forest with SGVA	20	22	–	–	–	12	27
6 Cortopassi-Laurino and Ramalho (1988)	*Am*	São Paulo – Brazil	23	–	–	–	–	13	18
	Ts	SGV	23	–	–	–	–	13	
7 Engel and Dingemans-Bakels (1980)	*Mfa*	Surinam / SGV	21	01	01	–	–	na	13
8 Guibu *et al* (1988)	*Mq*	São Paulo – Brazil / SGV	10	18	–	–	–	12	09
9 Imperatriz-Fonseca *et al* (1984)	*Ta*	São Paulo – Brazil / SGV	19	21	–	–	–	12	17
10 Imperatriz-Fonseca *et al* (1989)	*Am, Fs, Mm, Mq Pd, Pe, Pq, Pr, Ps, Ta, Ts*	São Paulo – Brazil / SGV	22	–	–	–	–	02	24
11 Imperatriz-Fonseca (1989)	*Pd*	São Paulo – Brazil /	04	04	–	–	–	04	32
	Pq	SGV	11	12	–	–	–	06	
	Fs		06	–	–	–		06	
	Pe		03	04	–	–		03	

Table I (continued)

Authors	Bee species	Place/Vegetation	No and type of samples: Stored pollen	Stored honey	Pollen loads	Nectar loads	Field observations	Period (months)	Bee plants*
12 Iwama and Melhem (1979)	*Ta*	São Paulo – Brazil / SGV	–	23	–	–	–	12	19
13 Kleinert-Giovannini and Imperatriz-Fonseca (1987)	*Mm*	São Paulo – Brazil / SGV	24	24	–	–	–	12	09
14 Knoll (1985); Knoll and Imperatriz-Fonseca (1987)	*Ta*	São Paulo – Brazil / SGV	–	–	–	–	na	12	14
15 Knoll (1990)	*Am, Mm,Mq,Nt Pd, Pe, Pq, Pr, Ps, Ta, Ts*	São Paulo – Brazil / SGV	–	–	–	–	na	12	62
16 Mouga (1984)	*Ps*	São Paulo – Brazil / SGV	13	13	–	–	–	13	12
17 Orth (1983)	*Mm, Mq, Pe, Pr Pq, Pqp, Sb, Ts*	Paraná – Brazil / SGVA and subtropical *Araucaria* forest	–	–	–	–	na	13	28
18 Ramalho *et al* (1985)	*Pr*	São Paulo – Brazil / SGV	17	29	–	–	–	12	10
19 Ramalho (1987);	*St*	São Paulo – Brazil / SGVA	01	01	–	–	–	na	06
Ramalho (1990)	*Sb*	São Paulo – Brazil / SGV	18	01	–	–	–	12	
	Sd		13	01	–	–	–	12	
	Sp		09	01	–	–	–	05	
20 Ramalho *et al* (1989)	*Mm*	São Paulo – Brazil /	04	–	–	–	–	04	13
	Mq	Atlantic rain forest	11	–	–	–	–	04	
	Mb	Paraná – Brazil /	01	–	–	–	–	na	
	Mq	Subtropical *Araucaria* forest zone	04	–	–	–	–	02	

Table I (continued)

Authors	*Bee species*	*Place/Vegetation*	*No and type of samples*					*Period*	*Bee*
			Stored pollen	*Stored honey*	*Pollen loads*	*Nectar loads*	*Field observations*	*(months)*	*plants**
21 Roubik *et al* (1986)	*Am, Mc, Mfas, Mful, Nt, Tat, Tb, Td, Tfe, Tj, Tm*	Central Panamá / Tropical monsoon vegetation	–	–	na	–	–	13(d)	10
22 Sakagami and Laroca (1971)	*Ts*	Paraná – Brazil / Secondary grassland within subtropical Araucaria forest zone	–	–	–	–	na	12	13
23 Sommeijer *et al* (1983)	*Am, Mfa, Mt*	Trinidad-West Indies	–	–	191	–	–	06	16

Abbreviations: *Am* = *Apis mellifera; Fs* = *Friesella schrottkyi; Fsi* = *Frieseomelitta silvestri; Mb* = *Melipona bicolor; Mc* = *Melipona compressipes; Mfas* = *Melipona fasciata; Mfa* = *Melipona favosa; Mfu* = *Melipona fasciata; Mful* = *Melipona fuliginosa; Mi* = *Melipona interupta; Mm* = *Melipona marginata; Mq* = *Melipona quadrifasciata; Mr* = *Melipona rufiventris; Mt* = *Melipona scutellaris; Ms* = *Melipona seminigra; Mtu* = *Melipona tumupasae; Nme* = *Nannotrigona mellaria; Nm* = *Nannotrigona minuta; Nt* = *Nannotrigona testaceicornis; Ot* = *Oxytrigona tataira; Pd* = *Plebeia droryana; Pe* = *Plebeia emerina; Pl* = *Ptilotrigona lurida; Pm* = *Partamona mourei; Pp* = *Partamona pseudomusarum; Pq* = *Plebeia saiqui; Pqp* = *Plebeia quadripunctata; Pr* = *Pleibeia remota; Ps* = *Paratrigona subnuda; Pv* = *Partamona vicina; Sb* = *Scaptotrigona bipunctata; Sd* = *Scaptotrigona depilis; Sp* = *Scaptotrigona postica; Spl* = *Scaptotrigona cf polysticta; St* = *Scaptotrigona tubiba; Ta* = *Tetragonisca angustula; Tam* = *Trigona amalthea; Tat* = *Trigona atomaria; Tb* = *Trigona barrocoloradensis; Tc* = *Trigona cilipes; Tch* = *Trigona chanchamayoensis; Td* = *Trigona dorsalis; Tfe* = *Trigona ferricauda; Tfu* =*Trigona cf fuscipennis; Tg* = *Tetragona goeltei; Tj* = *Trigona jatiformis; Tm* = *Trigona musarum; Tn* = *Tetragona nigra; Tpa* = *Trigona pallens; Ts* = *Trigona spinipes.* Stingless bee genera follow Camargo and Moure (1988). SGV = secondary growth vegetation with gardens. SGVA = secondary growth vegetation with monocultures or pastures. na = not available. * Refers to the number of important bee plants.

Table II. Important bee plants for stingless bees (*Melipona* and Trigonini) and Africanized honeybees *(Apis mellifera)* in neotropical habitats. Reference numbers are indicated in table I. (See *Methods* for explanation on selection of important bee plants). P = pollen; N = nectar. + and x = species or genus, respectively, listed in the Directory of Important World Honey Sources (Crane *et al*, 1984). ■ Data from studies with Africanized *Apis mellifera* (Santos, 1974; Roubik *et al*, 1984; Barth, 1989; Ramalho *et al*, 1990).

Bee plants	*Ref*	*Stingless bees* Meli-pona	*Trigo-nini*	*Africanized Honeybees* A mellifera	*P*	*N*
Acanthaceae						
Eranthemum sp	15			x		
Thunbergia grandiflora	+ 15		x			
Agavaceae						
Agave sisalana	* 15		x	x		
Aizoaceae						
Mesembryanthemum spectabile	15		x			
Amaranthaceae						
Alternanthera sp	2	x				x
Iresine celosia	5		x			x
Anacardiaceae						
Lithraea molleoides	10 15		x		x	
Mangifera indica	+ 16		x		x	
Schinus terebinthifolius	+ 8 10 11		x	■		x
Spondias sp	* 5		x	■	x	x
Spondias mombim	+ 3 5 23	x	x	x	x	x
Spondias raldkoferri	* 21		x	x	x	
Tapirira guianensis	2 3	x	x		x	x
Toxicodendron verniciferum	5 14		x			
Araliaceae						
Didymopanax morototomi	7	x			x	
Tetrapanax papirifera	9 11		x		x	x
Avicenniaceae						
Avicennia germinans	+ 7	x			x	
Balsaminaceae						
Impatiens balsamina	11 15 18		x	x	x	
I *sultanii*	10 11 15		x	x	x	x
I *walleriana*	5		x		x	x
Bignoniaceae						
Jacaranda oxyphyla	4		x			
Parmentiera aculeata	5		x		x	
Spathodea campanulata	9		x		x	
Tabebuia umbellata	11		x		x	
Bixaceae						
Bixa orellana	1	x			x	
Bombacaceae						
Chorisia speciosa	11		x		x	

Table II (continued)

Bee plants	*Ref*	*Stingless bees* Meli-pona	*Trigo-nini*	*Africanized Honeybees* A mellifera	*P*	*N*
Boraginaceae						
Cordia alliodora	+ 5		x		x	x
Burseraceae						
Protium heptaphyllum	1 2 3	x	x		x	x
P tenuifolium	21		x	x	x	
Cannaceae						
Canna indica	17		x			
Caprifoliaceae						
Sambucus australis	9 11 19		x		x	
Caricaceae						
Carica papaya	+ 5		x		x	x
Caryophyllaceae						
Silene armeria	14 15	x	x			
Celastraceae						
Maytenus evonimoides	10		x		x	
Clethraceae						
Clethra sp	* 5		x		x	x
Compositae						
Ageratum houstonianum	5		x			x
Ambrosia type	9		x			
Aster laevis	15			x		
Baccharis sp	* 4 15 21		x	x ■		
Baccharis sl	6 19		x	x	x	
B elaeagnoides	17		x			
B erioclada	17	x	x			
B helicrysoides	17		x			
B meridionales	17	x	x			
B oxyodonta	17		x			
B semiserrata	17	x	x			
B spicata	4 22		x			
Bidens sp	* 12		x	■		x
B pilosa	+ 11 15		x	x	x	
Chrysanthemum type	11		x		x	
Chysanthemum maximum	15		x			
Cirsium vulgare	18	x	x			
Coreopsis grandiflora	* 15			x		
Coryzia bonariensis	18	x	x			
Dahlia sp	14 15		x	x		
Emilia sonchifolia	11 15		x	x	x	
Eupatorium laevigatum	* 15			x		
E litorale	* 22		x			
Helianthus sp	* 15			x		
Hypochoeris brasiliensis	17		x			
Mikania sp	* 1	x		■	x	
M glomerata	* 6 15			x	x	

Table II (continued)

Bee plants	*Ref*	*Stingless bees* Meli-pona	*Trigo-nini*	*Africanized Honeybees* A mellifera	*P*	*N*
M roraimensis	* 2	x				x
Senecio sp	22		x			
S brasiliensis	15			x		
S oleosus	22		x			
Sonchus sp	15			x		
S oleraceus	17		x			
Taraxacum officinale	+ 17	x	x			
Vernonia sp	* 15			x ■		
V canescens	* 5		x			
V nitidula	* 17		x			
V polyanthes	+ 15			x		
V scabra	* 1	x			x	
Wedelia fertilis	5		x		x	x
W paludosa	15			x		
Convolvulaceae						
Ipomoea sp	* 4		x			
I cairica	* 15			x		
Crassulaceae						
Bryophyllum sp	11		x		x	x
Kalanchoe tubiflora	11		x		x	
Cruciferae						
Raphanus sativus	17	x	x			
Cucurbitaceae						
Momordica charantia	7 23	x	x	x	x	
Cyperaceae						
Cleome spinosa	14	x				
Dilleniaceae						
Davilla sp	3	x	x		x	
Elaeocarpaceae						
Muntigia calabura	10		x		x	
Ericaceae						
Rhododendrum indicum	14 15	x	x			
R simsi	4		x			
Euphorbiaceae						
Acalypha wilkesiana	8 16	x	x			x
Alchonea discolor	2 3	x			x	x
A latifolia	5		x			x
A sidaefolia	9 10 11 13 16	x	x		x	x
A triplinervia	12		x			x
Croton sp	* 22		x			
C lundianus	* 14 15	x	x	x		
C myrianthum	* 4		x			
Dalechampia sp	10 11		x		x	
Euphorbia milli	* 10 11		x		x	x
E prunifolia	* 17	x	x			
E pulcherrima	* 15			x	x	
E splendens	* 9 15	x	x		x	x

Table II (continued)

Bee plants	*Ref*	*Stingless bees* Meli-pona	*Trigo-nini*	*Africanized Honeybees* A mellifera	*P*	*N*
Hura crepitans	23		x	x	x	
Ricinus communis	4 6 11		x	x	x	
Sebastiania cf serrata	10		x		x	
Gramineae						
Coix *lacrima-jobi*	4		x			
Guttiferae						
Tovomitopsis nicaraguensis	21	x			x	
Vismia guianensis	2	x				x
Humiriaceae						
Humiria balsamifera	7	x			x	
Iridaceae						
Galidorea campestris	4		x			
Dietes vegeta	15			x		
Labiatae						
Coleus sp	14	x				
Cumilla galioides	22		x			
Hyptis brevipes	* 2	x				x
Iboza riparia	14 15	x	x			
Leonorus sibiricus	+ 22		x			
Ocimum kilimandscharicum	14	x	x	x		
Origanum vulgare	15			x		
Salvia sp	*15		x	■		
S paranaensis	* 4 23		x		x	
S splendens	* 15		x			
Lecythidaceae						
Gustavia superba	20	x			x	
Leguminosae						
Acacia sp	* 10 11 20	x	x	■	x	
Acacia podalyriaefolia	* 15			x		
Aeschynomene type	6	x			x	
Andira anthelminthica	* 11		x	x	x	
Bauhinia p	15			x		
B variegata	15		x			
Cassia sp	* 3	x	x	■	x	
Cassia laevigata	* 4 22		x			
C siamea	+ 2	x				x
Caesalpinia pelthophoroides	* 6 12		x	x	x	x
Calliandra brevipes	* 15			x		
C tweedi	* 15			x		
Crotalaria lanceolata	14 15	x	x			
Dalbergia sp	* 12		x			x
Delonix regia	23		x	x	x	
Desmodium sp	15			x		
Erythrina speciosa	15			x		
Inga edulis	* 1 15	x		x	x	
Leucaena glauca	16		x		x	
L leucocephala	6			x	x	
Lonchocarpus sp	5		x		x	x

Table II (continued)

Bee plants	*Ref*	*Stingless bees* Meli-pona	*Trigo-nini*	*Africanized Honeybees* A mellifera	*P*	*N*
Mimosa sp	* 7	x			x	
M asperula type	* 23	x	x		x	
M bimucronata	* 8 11	x				x
M dalleoides	* 13 10 11 15	x	x	x	x	x
M dollens	* 4		x			
M invisa	* 2	x				x
M micropteris	* 4		x			
M aff pudica	* 5		x			x
M pudica type	* 23			x	x	
M pudica	* 3 7 23	x			x	x
M scabrella	+ 20	x		■	x	
M velloziana	* 6 8 11 15	x		x	x	x
Myroxylum balsamum	9 11 13 16	x	x		x	x
Piptadenia sp	9 11 18	x	x	■	x	x
P gonoacantha	10 16 19 20	x	x	■	x	x
P rigida	12		x			x
Prosopis type	* 23	x	x		x	
Schizolobium sp	20	x			x	
S parahyba	10	x	x		x	
Sesbania sp	16		x		x	
Sophora tomentosa	15		x			
Stryphnodendron guianensis	3	x	x		x	
Tamarindus indica	+ 23		x		x	
Tipuana speciosa	+ 6 9 10 16 18	x	x	x	x	
Trifolium campestre	* 17		x			
Zornia sp	15			x		
Liliaceae						
Allium cepa	17		x			
Aloe sp	* 6 9 10 11 15 16		x		x	
Asparagus sl	6 18		x		x	
Asparagus-sp	8 11	x	x		x	x
A *plumosus* sl	2 8	x			x	x
Hemerocallis fulva	15		x			
Loranthaceae						
Phthirusa micrantha	2	x				x
Lythraceae						
Lafoensia nummularifolia	4		x			
Malpighiaceae						
Byrsonima sp	* 2	x			x	
B coriaceae	* 7	x			x	
B intermedia	* 12 15 16		x		x	x
Stigmaphyllon cf ellipticum	21		x		x	
Malvaceae						
Sida sp	5		x		x	x

Table II (continued)

Bee plants	*Ref*	*Stingless bees* Meli-pona	*Trigo-nini*	*Africanized Honeybees* A mellifera	*P*	*N*
Melastomataceae						
Aciotis type	23			x	x	
A dichotoma	7	x			x	
Miconia sl	8	x			x	x
Miconia sp	1 2 3 11	x	x		x	x
Miconia type	13	x			x	x
M cinerascens	17	x				
Tibouchina type	13	x			x	x
Tibouchina sp	6 8 9 11	x	x	■	x	x
T chamissoana	12		x			x
T holoserica	15		x	x		
T longifolia	5		x	x		
Meliaceae						
Cabralea sl	18		x			
Cedrela fissilis	10		x		x	
Moraceae						
Cecropia sp	3 4 6 9 18	x	x	x ■	x	x
C adenopus	10 11	x	x	x	x	x
C insignis	21	x			x	
C obtusifolia	5		x		x	
C peltata	23	x	x	x	x	
Chlorophora tintoria	23		x		x	
Coussapoa purpusii	5		x		x	
Morus nigra	9 13 16	x	x		x	
Pourouma guianensis	20			x	x	
Sorocea bonplandii	12		x			x
Musaceae						
Musa sp	+ 4		x			
Myrtaceae						
Campomanesia guazumaefolia	20	x		■	x	
Eucalyptus spp	* 8 9 10 11 12 13 16 18 19	x	x	x■	x	x
E blackelyi	* 6 12		x	x	x	x
E cinerea	* 12		x			x
E robusta	+ 6 12		x	x	x	x
E rudis	* 12		x			x
E tereticornis	+ 12		x			x
Eugenia spp	* 2 3 20	x	x	■	x	x
E pitanga	* 14	x				
Myrciaria caulliflora	19		x		x	
Psidium guajava sl	8	x				x
P guajava	+ 6 10 13	x		x ■	x	x
Syzygium cumini	+ 7	x			x	
S *jambos*	* 15		x			
Nyctaginaceae						
Bouganvillea spectabilis	8		x			x
Pisonia aculeata	21			x	x	

Table II (continued)

Bee plants	*Ref*	*Stingless bees*		*Africanized*	*P*	*N*
		Meli-pona	*Trigo-nini*	*Honeybees* A mellifera		
Ochnaceae						
Ouratea sp	4		x			
Oleaceae						
Jasminum azoricum	14	x				
Plamae						
Archontophoenix sp	15 18		x	x		
A cunninghamia sl	6		x		x	
A cunninghamia	6 11		x		x	x
Bactris gosipaes	3		x		x	
Chamaedorea tepejilote	5		x		x	
Cocos nucifera	+ 5 23	x	x	x	x	x
Elaeis guineensis	+ 5		x		x	x
E oleifera	* 20	x	x	x	x	
Euterpe sp	20	x			x	
Maximilliana martiana	3	x	x		x	
Socratea durissima	20	x	x	x	x	
Phytollacaceae						
Petiveria alliaceae	5		x		x	
Polygonaceae						
Polygonum acuminatum	* 7	x			x	
Triplaris surinamensis	+ 23	x			x	
Proteaceae						
Grevillea banksii	* 15		x	x		
Panopsis type	7	x				
Rosaceae						
Prunus sp	* 22		x			
P brasiliensis	* 4		x			
P domestica	* 17		x			
P persica	* 15		x			
Pyrus malus	17		x			
Rubus urticaefolius	* 17		x			
Rubiaceae						
Borreria laevis	* 2	x			x	
B latifolia	* 17		x			
Chimarris parviflora	21	x			x	
Coffea arabica	+ 5		x	■		x
Diodia polymorpha	15	x				
Plicourea sp	22		x			
P marcgravii	17		x			
Posoqueria latifolia	20		x		x	
Warzewiczia coccinea	2	x			x	
Rutaceae						
Citrus sp	* 5 10 15		x	x ■	x	x

Table II (continued)

Bee plants	*Ref*	*Stingless bees* Meli-pona	*Trigo-nini*	*Africanized Honeybees* A mellifera	*P*	*N*
Sapindaceae						
Allophylus edulis	17	x				
Sapindus saponaria	+ 5		x		x	
Serjania erecta	* 4		x			
Sapotaceae						
Pouteria stipitata	21	x			x	
Saxifragaceae						
Escallonia megapotamica	22		x			
E montevidensis	4		x			
Scrophulariaceae						
Paulownia sp	9		x		x	
P tomentosa	12		x		x	
Solanaceae						
Capsicum sp	17	x				
Cestrum corymbosum	4 22		x			
Cyphomandra sp	17	x				
Datura candida	23			x	x	
Nicotiania tabacum	+ 15		x			
Solanum sp	13 7 8 10 11 17 20	x	x	■	x	x
S americanum	17	x				
S fiscifolium	23		x	x	x	
S sisymbriifolium	17	x	x			
S stramoniifolium	7	x			x	
S variabile	17	x	x			
Sterculiaceae						
Dombeya sp	* 4		x			
D burgessiae	* 14 15	x	x	x		
D wallichi	* 14 15	x		x		
Guazuma ulmifolia	5		x		x	x
Sterculia chicha	9 11		x		x	
Theaceae						
Camellia japonica	15		x			
Tiliaceae						
Heliocarpus donneli-smithii	5		x		x	x
Ulmaceae						
Trema micrantha	3 5 6 10 12	x	x	x	x	x
Ulmus mexicana	5		x		x	x
Umbelliferae						
Centela biflora sl	19		x		x	
Eryngium eburneum	22		x			
Fœniculum vulgare	9 11 15		x		x	x
Petroselium hortense	12		x		x	x
Velloziaceae						
Vellozia sp	15		x			
Verbenaceae						
Tectona grandis	23		x		x	
Violaceae						
Rinorea squamata	21	x			x	
Zingiberaceae						
Alpinia henryi	4		x			

sources from the South of Brazil (South America) up to the South of Mexico (North America). In addition to the studies referred to in table I, some field studies (Sakagami *et al*, 1967; Sakagami and Laroca, 1971; Roubik, 1978; Laroca *et al*, 1982; Knoll, 1990), and an extensive survey of the principal pollen sources for European and Africanized honeybees in the Central and Western parts of Panama (Roubik *et al*, 1984) confirm this trend.

The families mentioned above comprise ≈ 60 000 species. Except for Compositae, Labiatae and Leguminosae, with 25 000, 3 000 and 17 000 species respectively, the rest are mainly distributed in tropical and subtropical regions all over the world (Joly, 1977; Heywood, 1978). Species of Compositae and Labiatae are very abundant in woodlands, wooded grasslands, grassland and bushland formations of South America, but are poorly represented in the tropical rain forests. Species of Caesalpinoideae and Mimosoideae (Leguminosae) are also more common in the tropics and subtropics. The neotropics are distinguished as a zone in which Solanaceae is concentrated, as the second largest concentration of Euphorbiaceae and Palmae, and the main center for dispersion of Myrtaceae, together with Australia, as well as being noted for the presence of Melastomataceae, one of the largest families in South America.

Thus when a general view is taken, it is evident that the main pollen and nectar sources for stingless bees are to be found among the plant families which are best represented in neotropical habitats. Regional differences can be seen, nonetheless. For example, the families Ericaceae, Labiatae and Polygonaceae are important for bees in the subtropics or in the zones where the tropics meet the subtropics, as shown by studies conducted in the South of Brazil (Sakagami and Laroca, 1971, Laroca *et al*, 1982, Orth, 1983; Knoll, 1990). Compositae and Labiatae predominate as bee plants in areas with open vegetation, often under anthropic influence. Palmae is more important in forested intertropical zones.

The following genera were important for both stingless bees and Africanized honeybees virtually over the entire neotropical zone: *Alchornea, Baccharis, Cassia, Cecropia, Croton, Euphorbia, Miconia, Mimosa, Piptadenia, Solanum, Tibouchina, Trema* and *Vernonia*. The importance of *Cecropia* (Moraceae) is surprising in view of the supposedly anemophilous nature of this group, which is commonly found at the forest edge, on river banks, and in secondary forests throughout the neotropical zone. *Piptadenia* seems to be especially important for bees on the Atlantic coast of South America, from the South to the Northeast of Brazil. Other native genera frequently cited in the literature and which are regionally important are: *Spondias* (Anacardiaceae), *Protium* (Burseraceae), *Euphorbia* (Euphorbiaceae), *Byrsonima* (Malpighiaceae) and *Eugenia* (Myrtaceae).

Out of a total of approximately 288 plant species, 126, 52 and 25 plant species were important solely for Trigonini, *Melipona* and Africanized honeybee respectively. Fifty-three plant species were important both for Trigonini and *Melipona*. It should be noted that the information available for *Melipona* covers 13 species as opposed to that for Trigonini, which covers 36 species, so that the data are biased in favor of the latter group of bees. Finally, 58 species were simultaneously important for Africanized honeybees and stingless bees. In this case, there is an evident underestimation of the number of plant species that are important for both bee groups, in view of the small number of comparative studies (table I). Be that as it may, when only comparative studies are considered, Trigonini may appear to be a more generalistic flower visitor than *Melipona* (Roubik, 1978; Orth, 1983; Knoll, 1990; and table II). Roubik (1978) also notes that Trigonini seem to be a more generalistic flower visitor than Africanized honeybees in forest and savanna habitats of Amazonia.

Preferential relationships of stingless bees with some plant families also seem possible (table II). If the frequency with which plant families are important in the various habitats or areas under study (table I) is considered, the following overall picture emerges: the families Leguminosae, Myrtaceae, Palmae and Rubiaceae are important for Africanized honeybees, Trigonini and *Melipona;* Anacardiaceae, Balsaminaceae, Compositae, Euphorbiaceae, Labiatae, Moraceae, Proteaceae and Sterculiaceae are more important for Africanized honeybees and Trigonini than for *Melipona;* Ericaceae, Liliaceae and Umbelliferae are more important for Trigonini than for Africanized honeybees and *Melipona;* Mimosoideae (Leguminosae), Melastomataceae, and Solanaceae are more important for *Melipona* than for Africanized honeybees and Trigonini. This kind of definition is obviously circumstantial and has to be experimentally verified.

Stingless bees have perennial colonies with specific populations of varying size but, with some exceptions (*eg* some species of *Trigona*), far smaller than those of Africanized honeybee colonies. Seen from a cost-benefit angle, for stingless bee colonies of a small size, it is an advantage to exploit flowers less frequently visited by those with a larger population, while for the latter it may well be that the adoption of strategies which give them more of a competitive edge in productive resources (Johnson and Hubbell, 1974, 1975; Hubbell and Johnson, 1978) is their main method for meeting their energy needs. Thus it is no surprise to find that in a given local context most of the food is obtained from only a few plant groups (table I), despite the huge number of important floral sources available on a regional scale and the vast plant diversity in tropical forest habitats (even when subject to anthropic influence).

As regards the impact of Africanized honeybees on neotropical bee plants, and particularly on stingless bees, there are forecasts of local extinction (Roubik, 1978; Roubik *et al,* 1986). Roubik (1989) admits that "Africanized honeybees seem preadapted to invade and persist in mosaic tropical habitats which gives them advantages over native bees", mostly owing to their generalized nesting habits. These bees are also better adapted than European honeybees to foraging in conditions of low nectar availability (Rinderer *et al,* 1984, 1985), a situation which can be common at the forest edge and in open areas with unmanaged flora in the neotropics. Stingless bees are particularly abundant in regions of rain forest and subhumid forest zones of the neotropics, and are evidently adapted to the seasonal or apparently unforeseeable rhythms of flowering and variations in floral composition (as part of the high degree of diversity) in relatively close areas within neotropical forest habitats. It is not yet clear whether in such habitats the basis and pattern of food supply favors the Africanized honeybee's foraging strategies, although countless native plant species are important food sources for this bee.

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Résumé – Les plantes mellifères importantes pour les abeilles sans aiguillon (mélipones et trigones) et les abeilles africanisées dans les régions néotropicales : une synthèse. Cet article présente une synthèse des sources de nectar et de pollen pour les abeilles sans aiguillon dans les régions néotropicales (Amérique du Sud, sauf Patagonie et Amérique centrale). Seules ont été prises en compte les informations quantitatives concernant les visites de fleurs, ce qui permet de comparer la valeur des sources florales spécifiques pour les abeilles sans aiguillon et les abeilles africanisées (tableau I). La plupart des données ont été obtenues par l'analyse pollinique de la nourriture récoltée par les abeilles. Quelques études de terrain ont été utilisées pour les listes de plantes visitées par les 2 groupes d'abeilles. Les études ont été faites dans des régions avec des types de végétation variés, influencés parfois par la présence d'agriculture, de prairies ou par l'urbanisation. Certaines ont été menées dans des forêts naturelles, très peu dans des régions d'herbages ou de savane.

Les familles botaniques suivantes : Anacardiacées, Composées, Euphorbiacées, Labiacées, Légumineuses, Mélastomatacées, Moracées, Myrtacées, Palmées, Rubiacées et Solanacées, qui renferment le plus grand nombre d'espèces importantes, à la fois pour les abeilles sans aiguillon et les abeilles africanisées (tableau II), sont aussi parmi celles qui présentent la plus grande diversité dans les habitats néotropicaux. Les genres *Alchornea, Baccharis, Cassia, Cecropia, Croton, Euphorbia, Miconia, Mimosa, Piptadenia, Solanum, Tibouchina, Trema* et *Vernonia* sont importants pour les 2 groupes d'abeilles dans pratiquement toute la zone néotropicale.

Sur un total de 288 espèces de plantes, 126, 52 et 25 sont importantes pour uniquement les trigones, les mélipones et les abeilles africanisées, respectivement. Cinquante trois espèces sont importantes pour les trigones et les mélipones à la fois. Les informations disponibles pour les mélipones couvrent 13 espèces, alors qu'elles en couvrent 36 pour les trigones; les données sont donc biaisées en faveur de ces dernières. Comme cela peut toujours se produire quand on ne fait que des études comparatives, les trigones semblent être plus généralistes que les mélipones dans leurs visites de fleurs. Cinquante huit espèces sont importantes pour les 2 groupes d'abeilles, abeilles sans aiguillon et abeilles africanisés. Il y a une sous-estimation évidente du nombre d'espèces importantes pour les 2 groupes, étant donné le faible nombre d'études comparatives (tableau I).

En ce qui concerne l'impact des abeilles africanisées sur les plantes mellifères néotropicales et en particulier sur les abeilles sans aiguillon, on peut prévoir l'extinction locale de plantes données. Mais l'on ne sait pas encore si la base et les modalités de l'offre de nourriture dans les habitats forestiers néotropicaux favorisent les stratégies de butinage des abeilles africanisées, bien que de nombreuses espèces de plantes indigènes soient d'importantes sources de nourriture pour ces abeilles.

abeille africanisée / *Melipona* / *Trigonini* / plante mellifère / région néotropicale

Zusammenfassung – Wichtige Trachtpflanzen für Stachellose Bienen (Meliponen und Trigonen) und für Afrikanisierte Bienen an neotropischen Standorten : Eine Übersicht. Diese Arbeit bietet eine Übersicht über die Pollen- und Nektarquellen von Stachellosen Bienen an neotropischen (= südamerikanischen)

Standorten. Es wurden nur zahlenmäßige Informationen über den Blütenbesuch berücksichtigt, wodurch ein Vergleich des Wertes spezifischer Trachtblüten für Stachellose Bienen und für Afrikanisierte Honigbienen möglich wird (Tabelle I). Die meisten Daten wurden durch die Pollenanalyse der von den Bienen gesammelten Nahrung gewonnen. Außerdem wurden einige Feldbeobachtungen zur Aufstellung von Listen der von beiden Bienengruppen besuchten Pflanzenarten herangezogen. Die Untersuchungen wurden in Gebieten mit unterschiedlicher Vegetation durchgeführt, in einigen Fällen beeinflußt durch landwirtschaftliche Nutzung, Viehweide oder städtische Siedlungen. Andere wurden in ursprünglichen Wäldern durchgeführt und sehr wenige in Gebieten mit Grasland oder Savanne.

Die Pflanzenfamilien Anacardiaceen, Compositen, Euphorbiaceen, Labiaten, Leguminosen, Melastomataceen, Moraceen, Myrtaceen, Palmae, Rubiaceen und Solanaceen enthalten einerseits die größte Zahl wichtiger Arten sowohl für die Stachellosen wie für die Afrikanisierten Bienen (Tabelle II), anderseits zeigen sie aber die größte Vielfalt an neotropischen Standorten. Die Gattungen *Alchorea, Baccharis, Cassia, Cecropia, Croton, Euphorbia, Miconia, Mimosa, Piptadenia, Solanum, Tibouchina, Trema* und *Vernonia* sind für beide Bienengruppen in praktisch der gesamten neotropischen Zone wichtig.

Aus einer Gesamtheit von 288 Pflanzenarten sind 126 ausschließlich für die Trigonen von Bedeutung, 52 nur für Meliponen und 25 nur für Honigbienen. 53 Arten sind sowohl für Trigonen wie für Meliponen wichtig. Die zur Verfügung stehenden Informationen über Meliponen beziehen sich auf 13 Arten, diejenigen über Trigonen jedoch auf 36 Arten, so daß diese Gruppe in unseren Daten stärker vertreten ist. Wie immer es sich verhalten mag, wenn man nur die Vergleichsstudien heranzieht, so ergibt sich, daß die Trigonen beim Blütenbesuch stärkere Generalisten sind als die Meliponen. Für beide Bienengruppen, Stachellose Bienen und Afrikanisierte Honigbienen, waren 58 Pflanzenarten gleichermaßen wichtige Trachtquellen. Es besteht eine deutliche Unterschätzung der Zahl von Trachtpflanzen, die für beide Gruppen von Bedeutung sind, besonders wenn man die geringe Zahl vergleichender Studien berücksichtigt (Tabelle I).

Was die Auswirkungen der Afrikanisierten Honigbienen auf neotropische Bienenpflanzen und besonders auf die heimischen Stachellosen Bienen betrifft, so gibt es Voraussagen für ein lokales Aussterben bestimmter Arten. Aber es ist noch keineswegs klar, ob die Basis und das Muster des Nahrungsangebots in neotropischen Waldstandorten die Sammelstrategie Afrikanisierter Bienen begünstigt. Es ist zu bedenken, daß dieser Biene zahllose heimische Pflanzenarten als wichtige Nahrungsquellen zur Verfügung stehen.

Afrikanisierte Biene / *Melipona* / *Trigonini* / Bienenpflanzen / neotropische Zone

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