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

Table I (continued)

Authors	Bee species	Place/Vegetation	Stored pollen	Stored honey	No and type of samples	Field observations	Period (months)	Bee plants*
					Nectar loads			
					Pollen loads			
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 Mougá (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 <i>Araucaria</i> forest	-	-	-	na	13	28
18 Ramalho <i>et al</i> (1985)	Pr	São Paulo – Brazil / SGV	17	29	-	-	12	10
19 Ramalho (1987); Ramalho (1990)	St	São Paulo – Brazil / SGVA	01	01	-	-	na	06
	Sb	São Paulo – Brazil / SGV	18	01	-	-	12	
	Sd	São Paulo – Brazil / SGV	13	01	-	-	12	
	Sp	São Paulo – Brazil / Atlantic rain forest	09	01	-	-	05	
20 Ramalho <i>et al</i> (1989)	Mm	São Paulo – Brazil / Atlantic rain forest	04	-	-	-	04	13
	Mq	Paraná – Brazil / Subtropical <i>Araucaria</i> forest zone	11	-	-	-	04	
	Mb		01	-	-	-	na	
	Mq		04	-	-	-	02	

Table I (continued)

Authors	Bee species	Place/Vegetation	Stored pollen	Stored honey	Pollen loads	Nectar loads	Field observations	Period (months)	Bee plants*
21 Roubik et al (1986)	Am, Mc, Mfas, Mful, Mt, Tat, Tb, Td, Tfe, Tj, Tm, Ts	Central Panamá / Tropical monsoon vegetation	-	-	na	-	-	13(d)	10
22 Sakagami and Laroca (1971)		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 = *Friesella silvestris*; Mb = *Melipona bicolor*; Mc = *Melipona compressipes*; Mfas = *Melipona fasciata*; Mfa = *Melipona favosa*; Mfu = *Melipona fuliginosa*; Mf = *Melipona interrupta*; Mm = *Melipona marginata*; Mq = *Melipona quadrifasciata*; Mr = *Melipona rufiventris*; Mt = *Melipona scutellaris*; Ms = *Melipona seminigra*; Mtu = *Melipona turnipusae*; Nme = *Nannotrigona mellaria*; Nm = *Nannotrigona minuta*; Nt = *Nannotrigona testaceicornis*; Ot = *Oxytrigona tataira*; Pd = *Plebeia droryana*; Pe = *Plebeia emeirina*; Pl = *Ptilotrigona lurida*; Pm = *Partamona mourei*; Pp = *Partamona pseudomusarum*; Pq = *Plebeia saiqui*; Pqp = *Plebeia quadripunctata*; Pr = *Plebeia remola*; Ps = *Paratrigona subnuda*; Pv = *Partamona vicina*; Sb = *Scaptotrigona bipunctata*; Sd = *Scaptotrigona depilis*; Sp = *Scaptotrigona posita*; Spl = *Scaptotrigona cf. polysitica*; St = *Scaptotrigona tubiba*; Ta = *Tetragona 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 goeitei*; Tj = *Trigona jatlormis*; 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						
<i>Eranthemum</i> sp	15			x		
<i>Thunbergia grandiflora</i>	+ 15		x			
Agavaceae						
<i>Agave sisalana</i>	* 15		x	x		
Aizoaceae						
<i>Mesembryanthemum spectabile</i>	15		x			
Amaranthaceae						
<i>Alternanthera</i> sp	2	x				x
<i>Iresine celosia</i>	5		x			x
Anacardiaceae						
<i>Lithraea molleoides</i>	10 15		x		x	
<i>Mangifera indica</i>	+ 16		x		x	
<i>Schinus terebinthifolius</i>	+ 8 10 11		x	■		x
<i>Spondias</i> sp	* 5		x	■	x	x
<i>Spondias mombim</i>	+ 3 5 23	x	x	x	x	x
<i>Spondias raldkoferri</i>	* 21		x	x	x	
<i>Tapirira guianensis</i>	2 3	x	x		x	x
<i>Toxicodendron verniciferum</i>	5 14		x			
Araliaceae						
<i>Didymopanax morototomi</i>	7	x			x	
<i>Tetrapanax papirifera</i>	9 11		x		x	x
Avicenniaceae						
<i>Avicennia germinans</i>	+ 7	x			x	
Balsaminaceae						
<i>Impatiens balsamina</i>	11 15 18		x	x	x	
<i>I. sultanii</i>	10 11 15		x	x	x	x
<i>I. walleriana</i>	5		x		x	x
Bignoniaceae						
<i>Jacaranda oxyphylla</i>	4		x			
<i>Parmentiera aculeata</i>	5		x		x	
<i>Spathodea campanulata</i>	9		x		x	
<i>Tabebuia umbellata</i>	11		x		x	
Bixaceae						
<i>Bixa orellana</i>	1	x			x	
Bombacaceae						
<i>Chorisia speciosa</i>	11		x		x	

Table II (continued)

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

Table II (continued)

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

Table II (continued)

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

Table II (continued)

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

Table II (continued)

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

Table II (continued)

<i>Bee plants</i>	<i>Ref</i>	<i>Stingless bees</i> <i>Meli- pona</i>	<i>Trigo- nini</i>	<i>Africanized</i> <i>Honeybees</i> <i>A mellifera</i>	<i>P</i>	<i>N</i>
Ochnaceae						
<i>Ouratea</i> sp	4		x			
Oleaceae						
<i>Jasminum azoricum</i>	14	x				
Plamae						
<i>Archontophoenix</i> sp	15 18		x	x		
<i>A cunninghamia</i> sl	6		x		x	
<i>A cunninghamia</i>	6 11		x		x	x
<i>Bactris gosipaes</i>	3		x		x	
<i>Chamaedorea tepejilote</i>	5		x		x	
<i>Cocos nucifera</i>	+ 5 23	x	x	x	x	x
<i>Elaeis guineensis</i>	+ 5		x		x	x
<i>E oleifera</i>	* 20	x	x	x	x	
<i>Euterpe</i> sp	20	x			x	
<i>Maximiliana martiana</i>	3	x	x		x	
<i>Socratea durissima</i>	20	x	x	x	x	
Phytollacaceae						
<i>Petiveria alliaceae</i>	5		x		x	
Polygonaceae						
<i>Polygonum acuminatum</i>	* 7	x			x	
<i>Triplaris surinamensis</i>	+ 23	x			x	
Proteaceae						
<i>Grevillea banksii</i>	* 15		x	x		
<i>Panopsis</i> type	7	x				
Rosaceae						
<i>Prunus</i> sp	* 22		x			
<i>P brasiliensis</i>	* 4		x			
<i>P domestica</i>	* 17		x			
<i>P persica</i>	* 15		x			
<i>Pyrus malus</i>	17		x			
<i>Rubus urticaefolius</i>	* 17		x			
Rubiaceae						
<i>Borreria laevis</i>	* 2	x			x	
<i>B latifolia</i>	* 17		x			
<i>Chimarris parviflora</i>	21	x			x	
<i>Coffea arabica</i>	+ 5		x	■		x
<i>Diodia polymorpha</i>	15	x				
<i>Plicourea</i> sp	22		x			
<i>P marcgravi</i>	17		x			
<i>Posoqueria latifolia</i>	20		x		x	
<i>Warzewiczia coccinea</i>	2	x			x	
Rutaceae						
<i>Citrus</i> 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						
<i>Allophylus edulis</i>	17	x				
<i>Sapindus saponaria</i>	+ 5		x		x	
<i>Serjania erecta</i>	* 4		x			
Sapotaceae						
<i>Pouteria stipitata</i>	21	x			x	
Saxifragaceae						
<i>Escallonia megapotamica</i>	22		x			
<i>E montevidensis</i>	4		x			
Scrophulariaceae						
<i>Paulownia</i> sp	9		x		x	
<i>P tomentosa</i>	12		x		x	
Solanaceae						
<i>Capsicum</i> sp	17	x				
<i>Cestrum corymbosum</i>	4 22		x			
<i>Cyphomandra</i> sp	17	x				
<i>Datura candida</i>	23			x	x	
<i>Nicotiana tabacum</i>	+ 15		x			
<i>Solanum</i> sp	13 7 8 10 11 17 20	x	x	■	x	x
<i>S americanum</i>	17	x				
<i>S fiscifolium</i>	23		x	x	x	
<i>S sisymbriifolium</i>	17	x	x			
<i>S stramonifolium</i>	7	x			x	
<i>S variabile</i>	17	x	x			
Sterculiaceae						
<i>Dombeya</i> sp	* 4		x			
<i>D burgessiae</i>	* 14 15	x	x	x		
<i>D wallichii</i>	* 14 15	x		x		
<i>Guazuma ulmifolia</i>	5		x		x	x
<i>Sterculia chicha</i>	9 11		x		x	
Theaceae						
<i>Camellia japonica</i>	15		x			
Tiliaceae						
<i>Heliocarpus donneli-smithii</i>	5		x		x	x
Ulmaceae						
<i>Trema micrantha</i>	3 5 6 10 12	x	x	x	x	x
<i>Ulmus mexicana</i>	5		x		x	x
Umbelliferae						
<i>Centela biflora</i> sl	19		x		x	
<i>Eryngium eburneum</i>	22		x			
<i>Foeniculum vulgare</i>	9 11 15		x		x	x
<i>Petroselinum hortense</i>	12		x		x	x
Velloziaceae						
<i>Vellozia</i> sp	15		x			
Verbenaceae						
<i>Tectona grandis</i>	23		x		x	
Violaceae						
<i>Rinorea squamata</i>	21	x			x	
Zingiberaceae						
<i>Alpinia henryi</i>	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, La-

roca *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 : Anacardiaceae, 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 uni-

quement 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 africanisées. 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* / *Trigoni* / 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 Biengruppen 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), andererseits 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 Biengruppen 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 Biengruppen, 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* / *Trigoni* / Bienenpflanzen / neotropische Zone

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