Insect feeding preferences on Piperaceae species observed in São Paulo city, Brazil

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ABSTRACT. Insect feeding preferences on Piperaceae species observed in São Paulo city, Brazil. Piperaceae species have been placed among the basal angiosperm and are adapted to a variety of habitats including moist forests, secondary vegetation and dry high lands. The major anatomical/morphology features are of small trees, vines, and shrubs for *Piper* species, while the epiphytic and succulent characteristics are predominant forms among *Peperomia* species. Their secondary chemistry can be mostly represented by amides, phenylpropanoids/lignoids, and chromenes in addition to a phletoria of biosynthetically mixed-origin secondary compounds. Although several amides and lignans are known as insecticides, several phytophagous insects, among which some considered pests of economic importance, have been observed feeding vigorously on Piperaceae species. Herein we describe the feeding preferences of fourteen phytophagous species of Coleoptera, Lepidoptera and Hemiptera over approximately fifty Piperaceae species observed in São Paulo, SP, Brazil, in a long-term basis.

KEYWORDS. Host plant; Insect-plant interaction; *Piper*; secondary metabolites.

RESUMO. Preferências alimentares de insetos por espécies de Piperaceae, observadas na cidade de São Paulo, Brasil. As espécies de Piperaceae têm sido posicionadas entre as angiospermas basais e são frequentemente encontradas em habitats diversificados que incluem matas ciliares, vegetação secundária e campos rupestres. As espécies de *Piper* possuem hábitos de plantas herbáceas, arboretos e trepadeiras enquanto que, no caso de *Peperomia*, é freqüente o hábito de epífitas e suculentas. As classes de metabólitos secundários que caracterizam espécies de Piperaceae são amidas, fenilpropanóides/lignóides e cromenos, além de diversos outros de origem biossintética mista de menor representatividade. Apesar de muitos desses possuírem atividades inseticidas, diversos insetos fitófagos, alguns considerados pragas de importância econômica, foram observados alimentando-se de espécies de Piperaceae. Neste trabalho são relatadas as preferências alimentares de quatorze espécies fitófagas de Coleoptera, Lepidoptera e Hemiptera sobre aproximadamente cinqüenta espécies de Piperaceae observadas em São Paulo, SP, Brasil, durante um período de quatro anos.

PALAVRAS-CHAVE. Interações planta-inseto; metabólitos secundários; *Piper*; planta hospedeira.

Among the extraordinary diversity found within the order Insecta, representing nearly 60% of the biota on Earth, 46% have developed herbivorous habits during the evolutionary process (Cronin & Abrahamson, 2001). The successful co-adaptation between insects and plants was an evolutionary event that provided important advantages to plants especially when pollinization and seed dispersal are concerned. In addition to volatile attractants in flowers and fruits, secondary compounds in leaves also have assumed crucial importance in the life cycle of insects acting as juvenile and moulting hormones for their normal growth and developmental process (Harborne, 2001). Nevertheless, some of the plant secondary compounds act as potent toxins and limit the generalized herbivory posing severe restrictions to the insects to cope with and as a consequence the majority of herbivorous insects are adapted to a relatively limited number of plant species (Glendinning *et al.* 2002; Ward *et al.* 2003). Among the mechanism developed by insects to overcome such toxicity, the digestive process appeared to be the simplest and efficient process in which several degradation reactions takes place. Additionally, insects are capable to sequester and use them for their own defense against pathogens and predators or as pheromones (Nishida, 2002; Hartmann *et al.* 2005). Secondary compounds are also involved in the mediation process of the third trophic level in which parasitoids interact with host insects (Abrahanson & Weiss, 1997). Indeed, the concept of adaptation role for secondary metabolites under ecological and evolutionary approach between insects and plants is broadly accepted and almost all interaction has at some point involvement of secondary compounds (Fordyce & Agrawal, 2001; Harborne, 2001).

A detailed investigation of insect-plant interactions is required in order to reconstruct the evolutionary path and such approach should involve determination of behavior, major phytochemicals, and phylogenetic aspects (Becerra, 1997). Then, the first step to clarify such relationship is the identification of host plants and their phytophagous insects in natural habitats.

Piperaceae. The family Piperaceae together with the family Chlorantaceae have been considered as basal Angiospermae (Jaramillo *et al*. 2004). The genus *Piper* is the largest one, comprising more than 700 species (Parmar, 1997). Approximately 240 species of *Piper* L., 25 species of *Ottonia* Sprengel and two species of *Pothomorphe* Miquel have been described in Brazil (Yuncker, 1973, 1975).

Several Piperaceae species have been used in the medicine. In Jamaica, of the eleven known species, *P. aduncum* L. and *P. hispidum* Sw. are mentioned as medicinal for stomachaches and as insect repellents (Asprey & Thornton, 1954). The seeds of black pepper, *P. nigrum* L., originally from the African east, have worldwide use as seasoning, while their leaves, roots and seeds are used in the treatment of bronchitis, gastrointestinal diseases, venereal diseases and rheumatism.

The phytochemical investigations of Piperaceae species have shown the accumulation of several insecticidal compounds in *P. nigrum* L., *P. betle* L., *P. spirei* C. DC., *P. decurrens* C. DC. and *P. longun* L. (Park *et al*. 2002; Navickiene *et al.* 2000; Paula *et al.* 2000; Parmar *et al.* 1997; Chauret *et al.* 1996). On the other hand several insect species have been described as visitors/phytophagous/pollinators (Figueiredo & Sazima, 2000).

Only recently, the chemical ecology of *Piper* species has been addressed (Dyer *et al.* 2004) in which the hypothesis of ecological trade-offs in defenses was examined in *Piper cenocladum* C. DC. regarding its relationship with ants.

The major aim of this paper is to describe the investigations carried out during four years in which feeding preferences of fourteen insect species on over fifty Piperaceae species were observed. The study was addressed to record possible specificity preferences of Coleptera, Lepidoptera and Hemiptera on Piperaceae species.

MATERIAL AND METHODS

Study site. The study was performed between August 2000 and January 2004 at an experimental field (garden next to the Laboratory of Natural Product Chemistry – LNP, S 23°33'915''; W 46°43'671'') of the Institute of Chemistry of the Universidade de São Paulo and on the reserve (CUASO) at the Campus of the Universidade de São Paulo (São Paulo, SP, Brazil).

Insect species. The insect species were collected mostly at the experimental field and also in different sites in Brazil and were identified by the first author (SAV) and Drs. Cleide Costa (Museu de Zoologia, Universidade de São Paulo), Sergio Ide (Instituto Biológico de São Paulo), and Gustavo Accacio (Departamento de Zoologia, Instituto de Biociências, Universidade de São Paulo). Vouchers specimens (Table 1) are deposited in the Museu de Zoologia, USP (Brazil).

The feeding preference of insect species was determined by field and laboratory observations. The insect species reared in laboratory were maintained in cages for a month with diet consisting of leaves of Piperaceae under artificial light (17 h light - 7 h dark) and room temperature (24 to 27 ºC).

Plant Materials. Out of fifty Piperaceae species cultivated at LNP only *P. gaudichaudianu* Kunth, *P. regnellii* C. DC. and *Pothomorphe umbellata* (L.) Miq. were originally found in this area. Moreover, additional species in this site include *Virola sebifera* Aubl. and *V. oleifera* (Schott) A.C. Smith (Myristicaceae); *Araucaria angustifolia* (Bentol.) Kuntze (Araucariaceae); *Psidium guayava* L. (Myrtaceae); *Theobroma cacao* L. (Sterculiaceae) and *Cecropia spp*. (Cecropiaceae).

The leaves from Piperaceae species were collected in the Campus of the Universidade de São Paulo (Brazil) in December 2000 and were identified by Dr. Elsie F. Guimarães (Jardim Botânico do Rio de Janeiro - Brazil). A voucher specimen (*Piper callosum* C. DC, Kato-0175; *Piper solmsianum* C.DC, Kato-0369; *Piper richardiaefolium* Kunth, KATO-0290; *Piper arboreum* Yunck, KATO-0007; *Piper hispidum* Sw, KATO-0014; *Piper gaudichaudianum* Kunth, KATO-0031; *Piper aduncum* L., KATO-0077; *Piper crassinervium* Kunth, KATO-0091; *Peperomia urocarpa* Fisch. & Mey., KATO-0104; *Piper amalago* var. *medium* (Jacq.) Yunck, KATO-0110; *Piper hoffmannseggianum* Roem. & Schult., KATO-0127; *Piper macedoi* Yunck, KATO-0136; *Piper cernuum* Kunth, KATO-137; *Piper nigrum* L., KATO-0157; *Peperomia galioides* Humb., Bonpl. & Kunth, KATO-0168; *Piper tuberculatum* Jacq, KATO-0169; *Ottonia martiana* Miq., KATO-172; *Ottonia propinqua* Kunth, KATO-0177; *Piper macedoi* Yunck., KATO-0180; *Piper hemmendorffi* C. DC., KATO-0181; *Piper glabratum* Kunth, KATO-0185; *Piper tectoniifolium* Kunth, KATO-0192; *Piper chimonanthifolium* Kunth; KATO-0193; *Piper cubataonum* C. DC., KATO-0194; *Piper dilatatum* Rich., KATO-0195; *Piper schenckii* C. DC., KATO-0202; *Piper pseudopothifolium* C. DC., KATO-0211; *Peperomia oreophila* Hensch., KATO-0224; *Piper lhotzkyanum* Kunth, KATO-0226; *Pothomorphe peltata* (L.) Miq., KATO-0235; *Piper rivinoides* Kunth, KATO-0254; *Piper permucronatum* Yunck., KATO-0283; *Peperomia rupestris* Humb., Bompl. & Kunth, KATO-0284; *Peperomia arifolia* Miq., KATO-0285; *Piper xylosteoides* (Kunth) Steud., KATO-0289; *Peperomia alata* Ruiz & Pav., KATO-0291; *Peperomia glabella var. nervulosa* (C. DC.) Yunck., KATO-0293; *Peperomia serpens* (Sw.) Loud., KATO-0295; *Peperomia rotundifolia* (L.) Humb., Bompl. & Kunth, KATO-0300; *Peperomia circinnata* Link, KATO-0312; *Peperomia elongata* Kunth, KATO-0313; *Peperomia pereskiaefolia* (Jacq.) Humb., Bonpl. & Kunth, KATO-0314; *Peperomia betle* L., KATO-0333; and *Peperomia blanda* (Jacq.) Humb., Bonpl. & Kunth, KATO-0354; are deposited at the Herbarium of Instituto de Pesquisas Jardim Botânico do Rio de Janeiro; *P. regnellii* C. DC., Benevides S/n.SPF112.6.84, is deposited at the Herbarium of Instituto de Biociências da Universidade de São Paulo.

RESULTS AND DISCUSSION

During the first year most of the effort was to determine the feeding preferences for fourteen species of insects collected and to identify them and the respective host plants. The feeding mechanisms observed varied from chewing,

Fig. 1. Phytophagous insects associated to *Piper* species. The ecological aspects of each species are reported on the text. A, adult of *Conoderus fuscofasciatus* on leaf of *Piper solmsianum*; B, adult of *Naupactus bipes* on leaf of *P. gaudichaudianum*; C, nymphs of *Callocanophora* sp. on stem of *P. aduncum*; D, adults of *Chasmodia* sp. on fruit of *P. gaudichaudianum*; E, couple of *Sibovia sagata* on leaf of *P. regnellii*; F, nymphs of *Aethalium reticulatum* attended by ants on stem of *P. aduncum*; G, same as in F, but female adult protecting cluster of eggs; H, adult of *Membracis foliata* on fruit of *P. arboreum*; I, pupa of *N. bipes* collected on roots of *P. gaudichaudianum*; J, caterpillar of *Heraclides brasiliensis* on leaf of *P. solmsianum*; K, pupa of *Quadrus u-lucida* on leaf of *P. regnellii*, and L, pupa of *Heraclides hectorides* on stem of *P. solmsianum*.

sucking and piercing according to the insect order (Table 2). Next, the major classes of secondary metabolites accumulated in each Piperaceae species has been examined based on previous phytochemical investigations carried out by our group. The occurrence of amides, lignans, neolignans, prenylated benzoic acid, chromene, phenylpropanoids, terpenoids, pyrones, flavones and chalcones have been reported (Alécio *et al*. 1998; Benevides *et al*. 1999; Baldoqui *et al*. 1999; Navickiene *et al*. 2000; Martins *et al*. 2000; Martins *et al*. 2003; Lago *et al*. 2004; Kitamura *et al*. 2006; Kato & Furlan, 2007).

Feeding preferences of Coleoptera species. The preliminary field observations revealed the presence of the weevil *Naupactus bipes* in four adult specimens of *Piper gaudichaudianum* Kunth in which about seventy adults have been observed. However, some individuals were also observed feeding on leaves of *P. arboreum* var. *hirtellum* Yuck, *P. aduncum* L., *P. hispidum* Sw. and *P. regnellii* C. DC.

The specificity of feeding habit of beetle was further investigated by means of multiple-choice tests under laboratory conditions. Ten specimens of *N. bipes* were maintained in a cage containing fresh leaves of *Piper hispidum* Sw., *P. arboreum* var. *hirtellum* Yunk, *P. gaudichaudianum* Kunth, *P. aduncum* L. and *P. regnellii* C. DC. during the period of one week. After two days leaves of *P. gaudichaudianum* Kunth were significantly (about 30% of leaf area) eaten by the beetles. Next, when the leaves of *P. gaudichaudianum* were removed, the beetles started to feed only on *P. regnellii* C. DC. Finally, when the leaves of *P. regnellii* C. DC. were removed the beetles stopped to eat during the following four days.

During the following generations, we found several larvae *N. bipes* in the roots of *P gaudichaudianum* Kunth and *P. regnellii* C. DC. These results associated to the feeding behavior of adults on leaves of *Piper* species indicated that the beetle species have a narrow relationship with these plant species.

The life cycle of *N. bipes* is annual and the presence of adult beetles coincides with the fructification period of *P. gaudichaudianum* Kunth from September to January. Its feeding preference under field conditions has remained precisely the same during the four generations. Although some beetle species such as *N. bipes, N. basilicus* and *N. versatilis* are considered polyphagous pests (Nora & Reis Filho, 1989; Reis Filho & Nora, 1988) they revealed a clear feeding preference for prenylated benzoic acid accumulating *Piper* species (Table 2).

The weevils *N. basilicus* (Germar, 1824) and *N. versatilis* (Hustache, 1947) had feeding preference by *P. gaudichaudianum* Kunth in which adults and larvae were also observed on the leaves and roots, respectively.

Individual male and female leaf chafer *Chasmodia* sp. were observed on fruits of *P. gaudichaudianum* Kunth during its mating. Larvae of *Conoderus* spp. are soil-dwelling that feed on small roots and bore into underground portions of stem causing plants to wither and die but virtually no information regarding the food preferences for adults is available. Apparently they cause minor damage by feeding on tender plant tissues, such as leaves and flower buds (Lawrence, 1991; Lima, 1953).

Feeding preferences of Lepidoptera species. The caterpillars of *H. hectorides* (Esper, 1794), *H. brasiliensis* (Rothsch & Jord, 1906) and *Q. u-lucida* (Plötz, 1884) feeding on leaves from *Piper* spp. appeared naturally at the experimental site. The three species showed a narrow chemical specificity by leaves from *Piper* species accumulating lignans or neolignans (Table 2). The caterpillars of *Q. u-lucida* were observed feeding on leaves from *P. regnellii* C. DC. (*N* = 40), *P. solmsianum* C. DC. (*N* = 15), *P. callosum* C. DC. (*N* = 3) and *P. richardiaefolium* Kunth (*N* = 4). The main host is *P. regnellii* C. DC. with caterpillars, pupae and oviposition by adult on leaves occurring throughout the year, except during July and August. The caterpillars of *H. hectorides* were observed feeding on leaves of *P. regnellii* C. DC. (*N* = 6) and *P. solmsianum* C. DC. (*N* = 3), while the caterpillars of *H. brasiliensis* were observed feeding only on leaves of *P. regnellii* C. DC. (*N* = 7).

Table I. Species of insects observed feeding on Piperaceae species.

Code species	Insects species
CSR001	1. *Naupactus bipes* (Germar, 1824), Coleoptera – Curculionidae
CSR002	2. *Naupactus basilicus* (Germar, 1824), Coleoptera – Curculionidae
CSR003	3. *Naupactus versatilis* (Hustache, 1947), Coleoptera – Curculionidae
CSR004	4. *Chasmodia* sp., Coleoptera – Scarabaeidae
CSR005	5. *Quadrus u-lucida* (Plötz, 1884), Lepidoptera – Hesperiidae
CSR006	6. *Heraclides hectorides* (Esper, 1794), Lepidoptera – Papilionidae
CSR007	7. *Heraclides brasiliensis* (Rothsch & Jord, 1906), Lepidoptera –Papilionidae
CSR008	8. *Conoderus fuscofasciatus* (Eschscholtz, 1829), Coleoptera – Elateridae
CSR009	9. *Edessa meditabunda* (Fabricius, 1794), Hemiptera – Pentatomidae
CSR010	10. *Membracis foliata* L., 1767, Hemiptera – Membracidae
CSR011	11. *Sibovia sagata* (Sigworet, 1859), Hemiptera – Cicadellidae
CSR012	12. *Callocanophora* sp., Hemiptera – Membracidae
CSR013	13. *Aethalion reticulatum* (L., 1767), Hemiptera – Aethalionidae
CSR014	14. *Sibaria armata* (Dallas, 1851), Hemiptera – Pentatomidae

The caterpillars feeding on leaves from *Piper* species were also observed in other sites. The *H. hectorides* (*N* = 4) and *Q. u-lucida* (*N* = 3) on *P. solmsianum* C. DC. (Ubatuba – SP, Brazil, S 23°27’731’’ W 45°11’760’’), *H. hectorides* on *P. solmsianum* C. DC. (*N* = 4) (Poços de Caldas, MG, Brazil, S 21º58'300’’ W 46º22’296’’), *H. hectorides* on *P. solmsianum* C. DC. (*N* = 4) and *P. regnellii* C. DC. (*N* = 3) (São Paulo, SP, Brazil, S 23º33’906" WO 46º43’634") and *H. hectorides* on *Piper* sp. (*N* = 9) (Itabuna, BA, Brazil).

Larvae of *H. brasiliensis* have been observed feeding on many species of Piperaceae (Tyler *et al.*, 1994), but can be also found on Rutaceae including cultivated *Citrus* spp; larvae of *H. hectorides* was reported feeding on *Piper amalago* L. but rarely on Rutaceae; larvae of *Q. u-lucida* feed on *Piper* spp., forming shelters by folding a single leave of the host and tying it with silk.

Feeding preference species of Hemiptera. The feeding

Table II. Relationship between insects and Piperaceae species and their major secondary metabolites.

Insect	Adult	Nymph	Larvae	Feeding Mechanisms	Piperaceae	Plant Secondary metabolites	References
Naupactus bipes	leaves		root	chewing	*P. gaudichaudianum*	PBA[a]	Lago *et al.* 2004.
	leaves		root		*P. regnellii*	BF[b] Neolignans	Benevides *et al.* 1999.
	leaves		root		*P. aduncum*	PBA	Baldoqui *et al.* 1999.
	leaves		root		*P. hispidum*	PBA	unpublished[d]
	leaves		root		*P. arboreum*	PBA	unpublished
N. basilicus	leaves		root	chewing	*P. gaudichaudianum*	PBA	Lago *et al.* 2004.
N. versatilis	leaves		root	chewing	*P. gaudichaudianum*	PBA	Lago *et al.* 2004.
Chasmodia sp.	fruit		root	chewing	*P. gaudichaudianum*	PBA	Lago *et al.* 2004.
Conoderus fuscofasciatus	leaves			chewing	*P. solmsianum*	THF[c] Lignans	Martins *et al.* 2000.
Quadrus u-lucida			leaves	chewing	*P. solmsianum*	THF Lignans	Martins *et al.* 2000.
			leaves		*P. richadiaefolium*	FF[d] Lignans	Unpublished
			leaves		*Piper* sp.	Lignans	unpublished
			leaves		*P. regnellii*	BF Neolignans	unpublished
			leaves		*P. callosum*	Lignans	unpublished
Heraclides hectorides			leaves	chewing	*P. regnellii*	BF Neolignans	Benevides *et al.* 1999.
			leaves		*P. solmsianum*	THF Lignans	unpublished
H .brasiliensis			leaves	chewing	*P. regnellii*	BF Neolignans	Benevides *et al.* 1999.
Membracis foliata	stem	stem		piercing and sucking	*P. arboreum*	PBA	unpublished
	stem	stem			*P. aduncum*	PBA	Baldoqui *et al.* 1999.
Sibovia sagata	leaves			piercing and sucking	*P. solmsianum*	THF Lignans	Martins *et al.* 2000.
Edessa meditabunda	leaves			piercing and sucking	*P. solmsianum*	THF Lignans	Martins *et al.* 2000.
Aethalium reticulatum	stem	stem		piercing and sucking	*P. tuberculatum*	Amides	Navickiene *et al.* 2000.
Callocanophora sp.	stem	stem		piercing and sucking	*P. gaudichaudianum*	PBA	Lago *et al.* 2004.
	stem	stem			*P. arboreum*	PBA	unpublished
	stem	stem			*P. aduncum*	PBA	Baldoqui *et al.* 1999.
Sibaria armata	fruit	fruit		piercing and sucking	*P. aduncum*	PBA	Baldoqui *et al.* 1999.
	fruit	fruit			*P. hispidum*	PBA	unpublished
	fruit	fruit			*P. arboreum*	PBA	unpublished
	fruit	fruit			*P. cernuum*	Dihydrocinnamic acids and lignans	Danellute *et al.* 2005.

[a]: Prenylated benzoic acids; [b]: benzofuran derivatives; [c]: tetrahydrofuran; [d]: inferences from ^1H NMR data from crude extracts.

preferences of six sap-sucking insects on Piperaceae species were analyzed and the stems were the tissue more heavily attacked (Table 2). The nymph and adult of *S. sagata* species were observed mainly on leaves of *Piper solmsianum* C. DC., *P. regnellii* C. DC. and *P. tuberculatum Jacq*; and also on fruits of *P. cernuum* Kunth. However, the presence of the nymph and adults does not always coincide with the fructification period of the *P. cernuum* Kunth. In the absence of the *P. cernuum* Kunth fruits, the insects appeared to migrate to the fruits of *P. hispidum* Sw. and *P. arboreum* var. *hirtellum* Yunck.

CONCLUSIONS

The analysis for specificity between fourteen insects and about fifty Piperaceae species revealed a remarkable narrow feeding preference. The caterpillar species (*Q. u-lucida*, *H. hectorides, H. brasiliensis*) were observed predominantly on lignan/neolignans-containing species such as *P. solmsianum* C. D C. and *P. regnellii* C. DC. In case of the beetles (*N. bipes, N. basilicus, N. versatilis, Chasmodia* sp., *C. fuscofasciatus*) and sap-sucking Hemiptera species (*M. foliata, S. sagata, E. meditabunda, A. reticulatum, Callocanophora* sp., *S. armata*), the preferred *Piper* species were *P. aduncum, P. gaudichaudianum* which contained prenylated benzoic acids as major compounds.

However, the precise ecological role of lignan/neolignans and benzoic acid derivatives as phagostimulant or as products to be sequestered by insects for defense or as hormones still remained to be determined but such specificity could indicate co-adaptation or even co-evolution.

Our results corroborated the evolutionary history of plants-insects, in which the majority of insects phytophagous are specifically associated with a limited number of vascular plants species (Harborne, 2001). Further investigations on the fate of secondary metabolites from each plant species during the digestive process of insects are on the way.

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