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Ants as dominant insect visitors of the extrafloral nectaries of sponge gourd plant, *Luffa cylindrica* (L.) (Cucurbitaceae)

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ABSTRACT. The button-shaped extrafloral nectaries (EFNs) located on the bracts, bracteoles, calyces and leaves of cultivated sponge gourd plant, *Luffa cylindrica*, were visited by insects belonging to five different orders: Hemiptera, Diptera, Coleoptera, Hymenoptera, and Lepidoptera. Insects with biological-control potential recorded at the EFNs included ants, wasps and ladybird beetles. Ants, comprising ten species, constituted by far the most abundant group (84.44 ± 4.34 % of individuals) at the EFNs. Insect pollinators included honey bees, butterflies and wasps, which, while visiting the floral nectaries (FNs), also visited the EFNs. Ants were found in large numbers on EFN-bearing plant parts, particularly leaves and calyces. Aggressive and abundant ant species visiting the plants included *Camponotus compressus*, *C. paria* and *Pheidole* sp. The major insect herbivore was the red pumpkin beetle, *Raphidopalpa foveicollis* Lucas, which fed predominantly on the corolla of the plants and, to a lesser extent, on each of the EFN-bearing vegetative parts. The low abundance of herbivores on vegetative parts indicates that the ants and, to a lesser extent, wasps, bees and ladybirds visiting the EFN-bearing plant structures may be aiding in crop plant protection from the herbivores. Thus, though the EFNs of sponge gourd plants attract predators, pollinators and also extrafloral nectar thieves such as flies, ants are the major group involved in the facultative association with the annual crop plant. Such studies may aid an environmentally-friendly management approach involving the natural enemies of insect pests of EFN-bearing annual crop plants.

Keywords: Extrafloral nectaries, insect visitors, sponge gourd plant, ants

INTRODUCTION

Extrafloral nectaries (EFNs) are nectar-secreting glands known to be present on a wide diversity of plants, particularly of tropical and sub-tropical habitats (Díaz-Castelazo *et al*. 2004). They are reported to occur in at least 66 plant families including angiosperms and ferns (Elias 1983; Schupp & Feener 1991). EFNs occur on both vegetative (e.g., young stem, leaves, petioles, stipules) and reproductive structures (e.g., buds, calyx inflorescence axis, flower peduncles, fruit) and are structurally diverse (Díaz-Castelazo *et al*. 2004). The morphology of EFNs on EFN-bearing plant taxa has been documented to vary extensively, being scale-like, stalk-shaped, pit-shaped, cup-shaped or button-shaped (So 2004; Díaz-Castelazo *et al*. 2005). Extrafloral nectar contains mainly sugar (15-75% by weight) along with small amounts of amino acids and other organic compounds (Elias 1983; Beattie 1985; Lanza 1988; Galetto & Bernardello 1992). EFNs are not directly involved with pollination but have been extensively documented to be visited by ants (Heil *et al*. 2001; Heil & McKey 2003) along with a few other insect taxa (e.g., flies, Hespenheide 1985; wasps, Cuautle & Rico-Gray 2003). Support for the protection hypothesis or the positive impact

of ants on the plants comes from many experimental studies showing increased herbivory and/or lower seed production when ants are excluded from plants (Janzen 1977; Tilman 1978; Schemske 1980; Koptur 1984; Oliveira 1997; Oliveira *et al.* 1999; Oliveira & Del-Claro 2005). However, very few studies have focused on arthropod diversity at the EFNs (Rudgers 2004), particularly of crop plants.

The present investigation was carried out to study the EFNs of sponge gourd plant, *Luffa cylindrica* (Linnaeus), and to find the EFN-visiting insect species at a locality in northeast India. Study of the diversity of insects attracted to the EFNs is extremely important, since indirect defence via tritrophic interactions is emerging as an important tool in environmentally-friendly crop protection strategy (Agarwal & Rastogi 2008a; Heil 2008). Sponge gourd is an important vegetable crop in India and information about potential pests, biological control agents, extrafloral nectar thieves etc., could facilitate more effective pest management. Since floral visitors which remove nectar but fail to effect pollination are considered nectar thieves (Stephenson 1982), EFN visitors which feed on the extrafloral nectar but fail to provide protection to the EFN-bearing plants may be regarded as extrafloral nectar thieves (Hespenheide 1985; Heil *et al.* 2004).

MATERIALS AND METHODS

Field investigations were carried out during the sponge gourd crop season in farmers' fields ($n = 5$, area =125 m^2 each) under normal agronomic practices for the region (including irrigation, weed harrowing, use of insecticides). For all observations, care was taken, using pitfall traps for ants and instantaneous scans of the plants for *Raphidopalpa* spp. (unpublished observations), that the normal abundance of ants and herbivores had been restored following each agronomic intervention. While the farmers used fast-degrading organophosphate insecticides (malathion, methyl parathion and quinalphos), mainly on the young (1–2 month old) crop, the observations were recorded on the mature (~3–4 month old) crop. The studies were conducted from February to July–August 2006, in Madhauli village, Varanasi (25°18´N, 83°01´E), Uttar Pradesh, India.

Sponge gourd plant, *Luffa cylindrica* (L.) (Cucurbitaceae), is a tendril-bearing annual crop plant with unisexual flowers, and the fruit is utilised as a vegetable in most parts of India. The various plant parts were examined for the occurrence of EFNs. A random selection of mature sponge gourd plants (50 plants per field) was monitored three times in a month (temporal replication), from 06:00 to 12:00 h during May 2006, to record the insect diversity.

All insects observed on the various plant parts—leaves, bracts, bracteoles, calyx, and corolla—were defined as visitors. Observations related to their feeding activities at the EFNs, floral nectaries (FNs) and other plant parts were also recorded. On the basis of their functional role and nutritive status (Kost & Heil 2005), insects were placed in one of four guilds: herbivores, pollinators, predators, and extrafloral nectar thieves (i.e., insects which remove the extrafloral nectar but fail to provide protection to the EFN-bearing plant from insect herbivores) (Table 1).

Abundance and types of insects visiting the EFNs and FNs of the unisexual flowers was recorded on randomly selected mature sponge gourd plants (25 plants per field). The observations, lasting about 90 seconds at each plant, carefully distinguished visits and feeding activities of insects at the EFNs (on extrafloral nectar) from those with feeding on EFN-bearing plant parts (but not EFNs), and activities on FNs from those on the corolla tissue. All insects were identified to family level and demarcated into morphospecies. The term "wasp" in the present study refers to species of the family Vespidae, since only these were observed at the EFNs of sponge gourd plants. Since worker ants (Family Formicidae) were found to be the most numerous on the plants, particularly at EFNs, they were identified to species level. For each of the ten ant species visiting the sponge gourd plants, abundance on each of the various plant parts, i.e., leaves, bracts, bracteoles, calyces and flowers, was recorded.

Table 1. Insect visitors recorded on the different plant-parts of the sponge gourd, *Luffa cylindrica*, plants. Abbreviations used: EFN—extrafloral nectar, FN—floral nectar.

Order	Taxon	Morpho-species	Plant-part used for feeding	Guild
Hemiptera	Pyrrhocoridae	1	Leaves, bracts, bracteoles, flowers	Herbivore
Diptera	Muscidae	1	EFN	Nectar thief?
	Calliphoridae	1	EFN	Nectar thief?
	Tachinidae	1	EFN	Nectar thief?
Coleoptera	Chrysomelidae	2	Leaves, bracts, bracteoles, calyces, flowers	Herbivores
Hymenoptera	Coccinellidae	1	EFN/FN	Predator
	Vespidae	2	EFN/FN	Predator/pollinator
	Apidae	2	EFN/FN	Pollinator
	Formicidae	9	EFN	Predators
	Tapinoma melanocephalum	-	EFN/FN	Predator
Lepidoptera	Nymphalidae	2	EFN/FN	Pollinators
	Pieridae	1	EFN/FN	Pollinator

Statistical analysis

An analysis of variance (two-way ANOVA followed by post-hoc Tukey HSD test) was applied to test the variation in the abundance of insect visitors between insect types and between plant parts (leaves, calyces, bract, bracteoles and corolla). Two-way ANOVA was also used to assess the variation in ant abundance between ant species and between plant parts. One-way ANOVA was used to test the variation in the number of insect visitors of different taxa, both on the EFNs and on the FNs of each plant.

RESULTS

Extrafloral nectaries of sponge gourd plants

EFNs were located on the leaves, bracts, bracteoles and calyces of the buds and unisexual flowers (Fig. 1). These were elevated, button-shaped structures. While actively producing nectar, each EFN developed a depression in the centre. The central, translucent glandular tissue produced and collected nectar in the central cup-shaped region of the nectary.

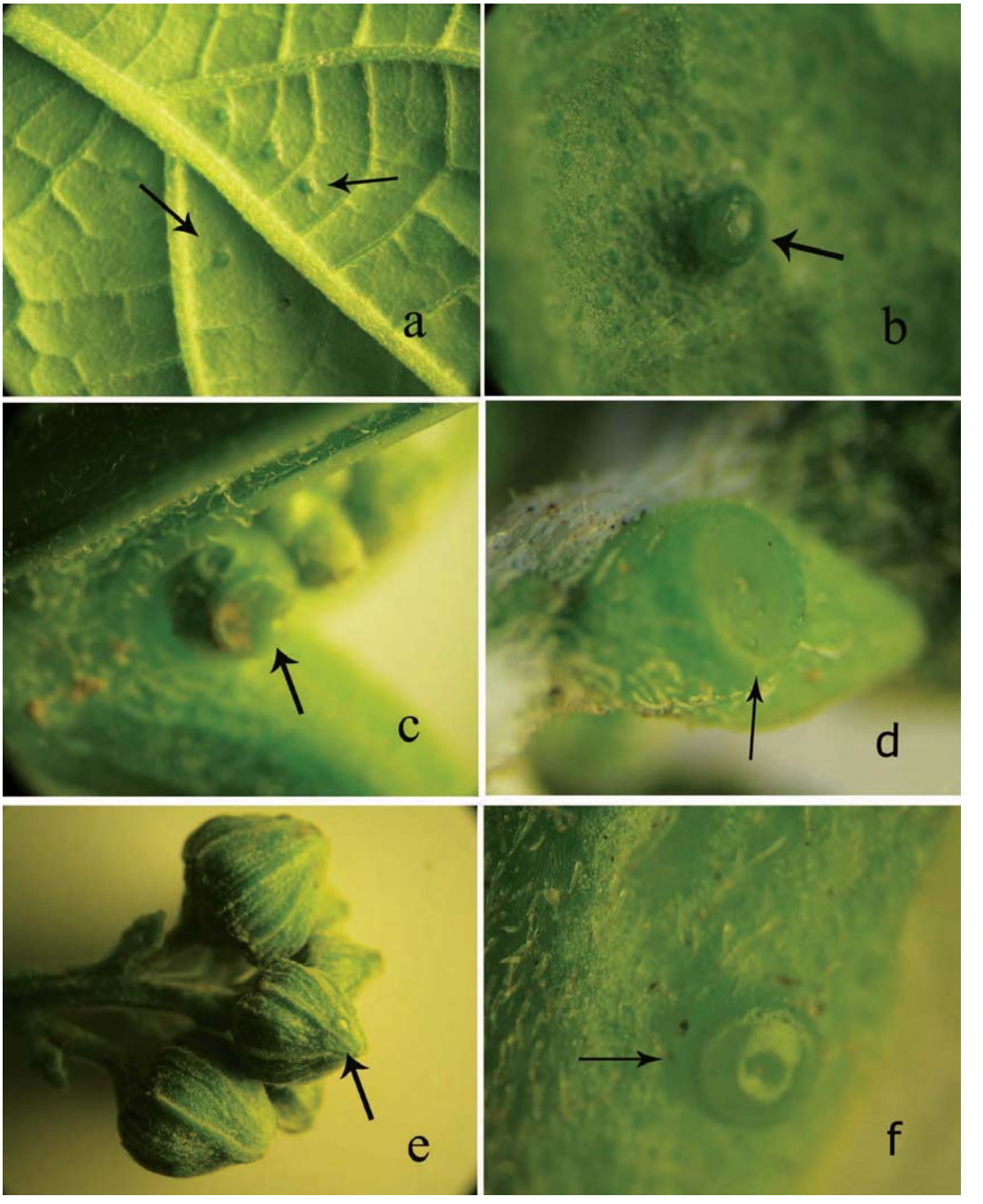

Fig. 1. Location of the elevated, button-shaped extrafloral nectaries on the different plant-parts of the sponge gourd plant, *Luffa cylindrica*: (a) leaf (28X), (b) enlarged view of the leaf (140X), (c) bract (140X), (d) bracteole (140X), (e) calyx of the flower bud (60X), and (f) calyx of flower (140X).

Insect diversity on the sponge gourd plants

Insects belonging to five orders were recorded on the sponge gourd plants. These included ants, wasps and bees (Hymenoptera), butterflies (Lepidoptera), red cotton bug *Dysdercus koenigii* Fabr. (Hemiptera), flies (Diptera), and the chrysomelid beetles *Raphidopalpa foveicollis* Lucas and *R. intermedia* Jacoby (Coleoptera) (Figs. 2 & 3). While ants were by far the most abundant visitors (mean ± SE, 71.43 ± 0.32 % of individuals on a plant, n = 250 plants), *Raphidopalpa* spp. were the most abundant insect herbivores (12.78 ± 0.12 % per plant) with *R. foveicollis* being the major insect pest. The relative abundance of other insect taxa observed on the plants—ladybird beetles, bees, wasps, butterflies, flies and bugs—was 5.81 ± 0.11 %, 1.39 ± 0.03 %, 2.55 ± 0.01 %, 1.85 ± 0.01 %, 2.55 ± 0.04 % and 1.62 ± 0.05 %, respectively.

Significant variation was found in both the abundance of different insect types and the abundance on different plant-parts (two-way ANOVA: insect types, $F_{8,180} = 36.38$; plant-parts, $F_{4,180} = 29.52$; $P < .0001$ in both cases), and the interaction between insect type and plant-part was also significant ($F_{32,180} = 32.89$; $P < .0001$). Ants had significantly greater abundance than other insect types on each of the five different plant-part types (Tukey's post-hoc test: $P < .0001$ in all cases) (Fig. 3). *Raphidopalpa foveicollis*, the major insect pest of sponge gourd, was significantly more abundant (Tukey's post-hoc test: $P < .0001$) on the corolla (35.5 ± 4.32 %) than on leaves (22.6 ± 2.31 %), bracts (12.9 ± 1.69 %), bracteoles (6.4 ± 0.87 %) or calyx (22.6 ± 3.2 %). In the case of the occasionally-occurring minor pest *R. intermedia*, the abundance of the beetles was significantly higher (Tukey's post-hoc test: $P < .0001$, in both cases) on the corolla (28.6 ± 1.92 %) and calyx (28.6 ± 3.2 %) than on leaves (14.3 ± 1.78 %), bracts (14.3 ± 2.18 %) or bracteoles (14.3 ± 1.66 %).

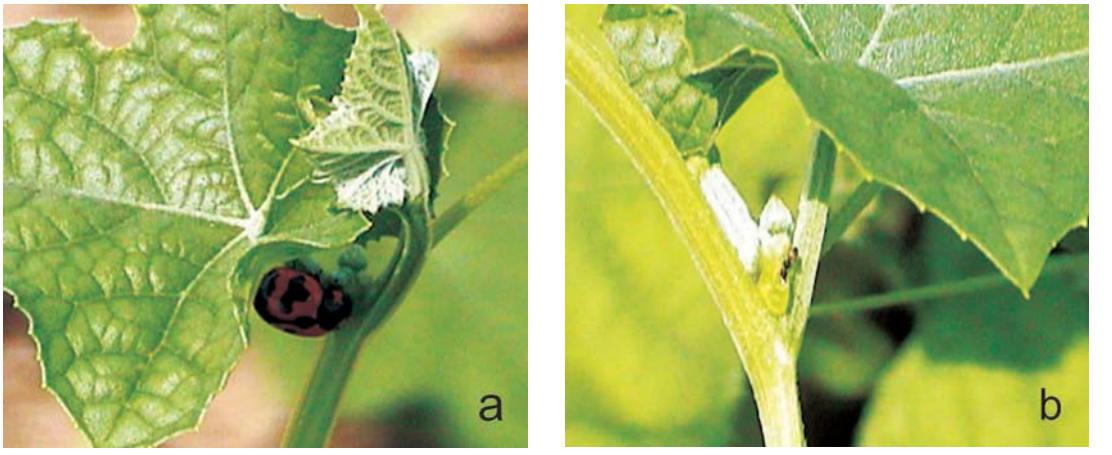

Fig. 2. Two of the insects recorded feeding at the extrafloral nectaries of sponge gourd plant, *Luffa cylindrica*: a) ladybird beetle, and (b) *Tapinoma melanocephalum* ant.

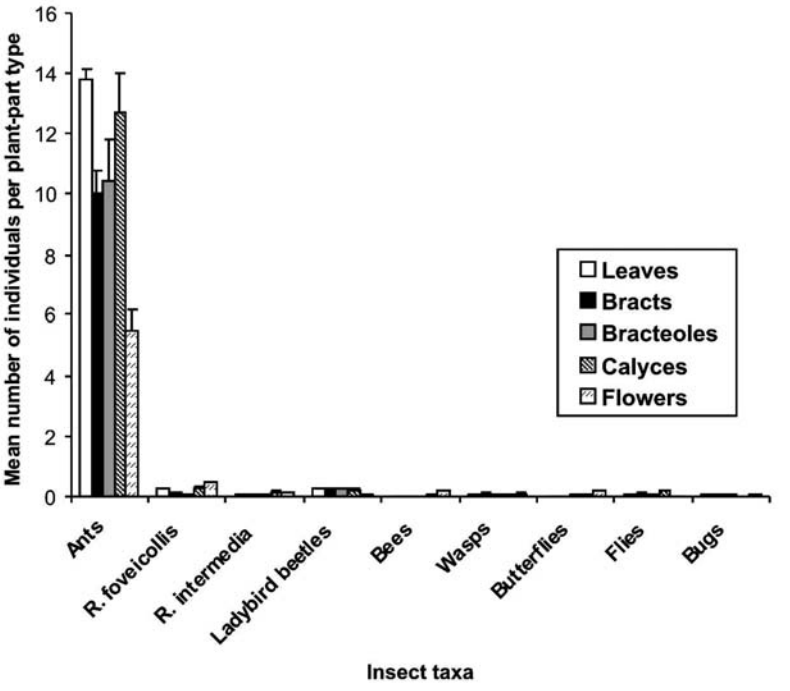

Fig. 3. Mean (± SE) number of insect visitors/plant on the various plant-parts: leaves, bracts, bracteoles, calyces, and flowers of the sponge gourd plants.

While *Raphidopalpa* spp. adults fed on the tissue (as evident from the small irregular holes made by them) and red cotton bug sucked the sap (evident from observation of piercing and sucking behaviour and from the tiny necrotic spots made on the plant-part-surface) of the EFN-bearing structures, neither were found to feed on the extrafloral nectar.

Ants occurred at particularly high relative abundance (84.44 ± 4.34 %) on EFNs. Ten ant species visited the sponge gourd plants: *Pheidole* sp., *Tetramorium* sp., *Aphaenogaster* sp. and *Monomorium latinode* (all Myrmicinae), *Pachycondyla tesserinoda* (Ponerinae), *Camponotus compressus*, *Camponotus paria*, *Camponotus infuscus* and *Camponotus sericeus* (Formicinae), and *Tapinoma melanocephalum* (Dolichoderinae) (Fig. 4). Significant variation in ant abundance was found between ant species and between plant-parts (two-way ANOVA followed by Tukey's HSD test: $F_{9,235} = 116.32$ for ant species; $F_{4,235} = 17.34$ for plant-parts; both $P < .0001$), and the interaction between the two factors was also significant ($F_{36,235} = 23.45$; $P < .0001$). Of the four most abundant ant species recorded on the plants, *Pheidole* sp. was most aggressive towards other plant-visiting arthropods. *Camponotus compressus* and *C. paria* were moderately aggressive while *T. melanocephalum* was a relatively timid ant species. With the exception of *T. melanocephalum* (which visited the FNs), all ant species were observed at the EFNs and very rarely on the petals. *Camponotus compressus* and *C. paria* were both significantly more abundant at calyces than at other plant-parts (Tukey's post-hoc test: $P < .01$ in each case). The tiny worker ants of *T. melanocephalum* were found to be significantly more abundant on the corolla than on other plant-parts ($P < .001$). *Pheidole* sp. was significantly more abundant on leaves than on bracts, bracteoles, calyces ($P < .05$) and corolla ($P < .001$). *Pachycondyla tesserinoda* and *Tetramorium* sp. were also more abundant on leaves than on the corolla ($P < .05$).

While bees and butterflies visited mainly the FNs, ants, wasps and ladybirds visited both

types of nectaries but predominantly EFNs. Flies, belonging to three dipteran families, fed only on extrafloral nectar, at the EFNs (Fig. 5). Significant variation was found in abundance between different insect taxa, at both the EFNs and FNs (one-way ANOVA: EFNs: $F_{5,20} = 21.56$; FNs; $F_{5,20} = 16.62$; $P < .0001$ in both cases. Ants had significantly higher abundance, on EFNs and FNs, than each of the other insect visitor categories (Tukey's post hoc test: $P < .001$ for all comparisons, in both cases). Although a higher abundance of bees and butterflies was recorded on FNs than on EFNs, no statistically significant differences were found.

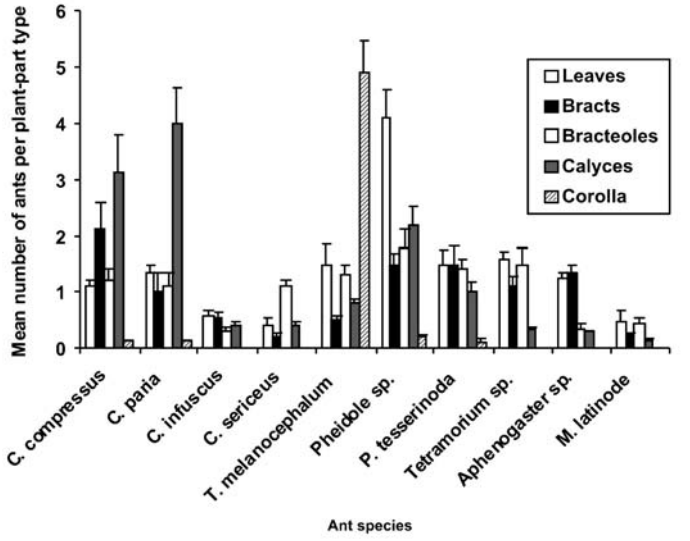

Fig. 4. Mean (± SE) number of ant visitors belonging to each of the ten ant species/plant, recorded on various plant-parts: leaves, bracts, bracteoles, calyces, and flowers of the sponge gourd plants.

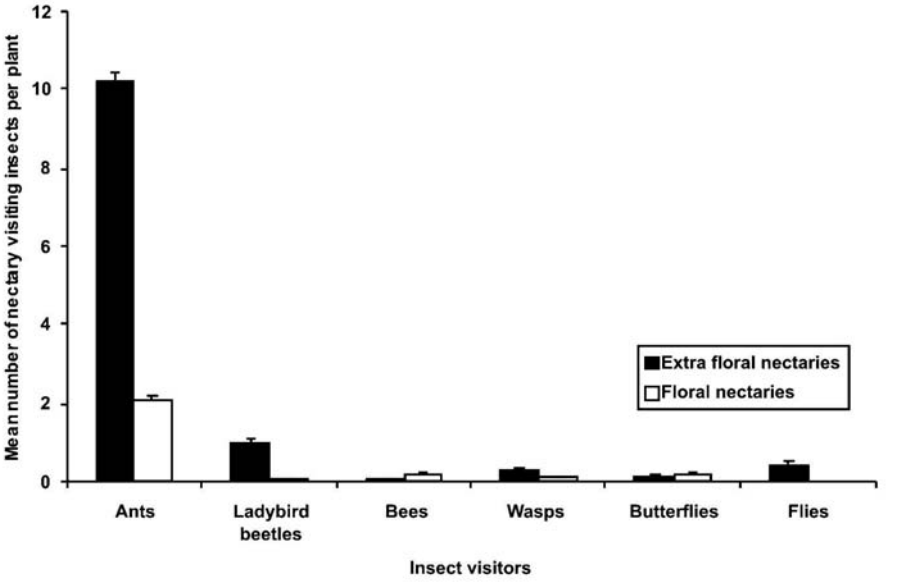

Fig. 5. Mean (± SE) number of insect visitors/plant on the extrafloral nectaries and floral nectaries of the sponge gourd plant.

DISCUSSION

The results of this investigation indicate ants to be the most abundant group of insect visitors on sponge gourd plants, and the most abundant group on EFNs in particular. This is in line with an earlier study in which ants comprised 60% of all nectary-visiting arthropods at the EFN-bearing Southeast Asian myrmecophilic plant, *Macaranga tanarius* (Heil *et al.* 2004). *Camponotus compressus, C. paria*, *Pheidole* sp. and *T. melanocephalum* were the most abundant species on the plants. While the tiny *T. melanocephalum* ants occurred predominantly on the FNs, the other ant species occurred on the EFNs and very rarely on the corolla. Since *Pheidole* sp., *Camponotus* spp., *P. tesserinoda* and *Tetramorium* sp. are highly- to moderately-aggressive generalist predators, observed to deter and reduce the residence time of the chrysomelid beetles *Raphidopalpa foveicollis* and *R. intermedia* on the plants (Agarwal & Rastogi 2008a, 2009), ants probably aid in reducing plant visits by these insect herbivores. The different ant species visited all the vegetative parts bearing EFNs. However, the most abundant and aggressive species including *Pheidole* sp. and *Camponotus* spp. (Agarwal *et al.* 2007; Agarwal & Rastogi 2008a) visited the leaves, bracts and calyces in greater number. *Tapinoma melanocephalum*, which was the only ant species to visit the flowers, has tiny, timid workers (Agarwal & Rastogi 2008b) which do not deter insect pollinators and have very low deterrent effect on the insect herbivores of sponge gourd plants (Agarwal & Rastogi 2008a). This may account for the greater number of *R. foveicollis* on the floral tissues than on other plant-parts which are protected to a considerable extent by the EFN-visiting ant species. A higher abundance on floral than vegetative parts is otherwise hard to explain, since these beetles cause extensive leaf defoliation in many cucurbits (Laghari *et al.* 2005).

Pollinators such as bees, butterflies and wasps supplement their floral nectar diet with extrafloral nectar. EFNs of sponge gourd plants are large, button-shaped structures. These produce visible nectar even during the high-temperature conditions of summer. Earlier studies have shown a positive correlation between the size of EFNs and nectar volume (Díaz-Castelazo *et al.* 2004; Rudgers 2004), suggesting a high volume of nectar production by the large sponge gourd nectaries. It is known that although wasps (Vespidae) hunt a variety of insects (Richter 2000), they also act as pollinators while visiting flowers for nectar (Solomon Raju *et al.* 2006). Still, although insects belonging to several taxonomic groups, including wasps and bees (Hymenoptera), flies (Diptera) and ladybirds (Coleoptera), were recorded at the EFNs in this study, it is likely that ants are the most important consumers of nectar from EFNs.

This is the first study of insect diversity at the EFNs of an annual vegetable crop plant in India. The results support earlier reports on the occurrence of ladybirds (Pemberton & Vanderberg 1993), bees (O'Dowd 1979), wasps (Bugg *et al.* 1989; Stapel *et al.* 1997), roaming spiders (even though mainly carnivorous: Taylor & Foster 1996; Ruhren & Handel 1999; Taylor & Pfannenstiel 2008), neuropterans (Limburg & Rosenheim 2001) and even birds (Pemberton 1993) on the EFNs of plants.

Flies recorded at the EFN-bearing structures are probably nectar thieves, as suggested in an earlier study of *Byttneria aculeata* in Costa Rica (Hespenheide 1985). No defensive function in protecting plants from insect herbivores has been attributed to flies (Kost & Heil 2005). In fact, they have been reported to actively exclude plant-protecting arthropods, such as ants, from nectaries (Heil *et al.* 2004), causing significant reduction in the indirect defence force mobilised by plants. Moreover, it is suggested that nectar theft may reduce the attractiveness of the plants to beneficial arthropods (Rudgers 2004).

Herbivores on the sponge gourd plants included the defoliators, red pumpkin beetle *R. foveicollis* and *R. intermedia*, along with the pyrrhocoreid red cotton bug *D. koenigii*, which is a sap sucker. While *R. foveicollis* is documented to be the most important leaf defoliator of sponge gourd, cucumber and pumpkin crops (Cucurbitaceae) in India (Laghari *et al.* 2005), *R. intermedia* is an occasional minor pest of cucurbits.

The generalist-predator ant species nesting and foraging in the study area, while preying on a variety of insect pests (Agarwal & Rastogi 2005; 2009), apparently supplement their

diet with carbohydrate-rich liquid food produced by the EFNs of the plants and in return provide protection to the plants by deterring insect herbivores (Agarwal & Rastogi 2008a).

Along with the ant visitors, a low abundance of predatory wasps and ladybirds, the latter being well-known biological-control agents of insect pests, was recorded at the EFNs of the vegetable crop plants. The role of EFNs in attracting other arthropod predators may become more important when ants are excluded, as shown by Mathews *et al*. (2009) for peach (*Prunus persica* (L.) Batsch) cultivars in USA whose EFNs attracted Araneae, Asilidae, Cantharidae, Coccinellidae and others to ant-excluded plants.

EFN-bearing sponge gourd plants, while presumably incurring a small loss of extrafloral nectar to flies, attract pollinators as well as potential 'bodyguards' (ants, ladybirds, wasps) which aid in plant propagation or protection. The results of this study may help in the utilization of natural enemies in devising environmentally-friendly pest management strategies of insect pests of crops in ephemeral annual systems. *Camponotus compressus* and *C. paria* were more abundant on the calyces while *Pheidole*, *Tetramorium* and *P. tesserinoda* were present in greater numbers on the leaves and *T. melanocephalum* was abundant on the corolla. These differences in the abundance of different ant species on different plant-parts may be due to competitive interactions among the plant-visiting ant species (unpublished observations). Niche differentiation among the plant-visiting ant species may thus facilitate protection to different plant-parts.

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