

# FIRST RECORD ON INTERACTION BETWEEN ANTS, OTHER INSECT VISITORS AND EXTRAFIORAL NECTARIES (EFNS) IN SELECTED CROPS FROM INDIA

# T. Nalini\* and R. Jayanthi

Department of Entomology, Faculty of Agriculture, Annamalai University, Chidambaram - 608002 (Tamil Nadu), India.

# Abstract

A study was conducted to know the interaction between ants, other insect visitors and extrafioral nectaries (EFNs) in selected crops at experimental farms of Faculty of agriculture, Annamalai University in which field incidence of ants, herbivores and predators in five EFN-bearing crops *viz., Vigna mungo, Vigna radiata, Gossypium hirsutum, Dolichos lablab* var. *typicus* and *Ricinus communis* were observed. Among the herbivores *Phenacoccus* sp., *Aphis* sp. and *Helicoverpa* sp. were highest and among predators Coccinellidae and Vespidae was highest. *Camponotus compressus* was highest in *Vigna mungo, Vigna radiata* and *Gossypium hirsutum*. In *Hibiscus cannabinus, Ricinus communis* and *Dolichos lablab* var. *typicus, Myrmicaria brunnea* and *Solenopsis geminata* was highest respectively. In ant - exclusion experiment, in both control and treatment *Phenacoccus solenopsis* showed gradually decreasing pattern from the first week to fourth week. But Coccinellidae and Mantidae showed increasing and fluctuating pattern during every consecutive week in control and treatment respectively. Parasitized mealybug mummies number (by the parasitoid, *Aenasius arizonensis* Hayat) showed decreasing and increasing pattern from first to fourth week in control and treatment respectively.

Key words : Field incidence, ants, herbivores, predators, EFN-bearing crops, ant - exclusion.

# Introduction

Extrafloral nectar (EFN) is secreted mainly on the most valuable organs, that is, organs that are characterized by strong future contribution to the fitness of the plant and high construction costs (such as young leaves, developing fruits, etc.), and the plant secretes EFN in much higher amounts in response to herbivore-infiicted damage, that is, when enemy pressure is high. Thus, EFN is secreted in a phenotypically plastic manner according to the predictions of the optimal defense hypothesis (ODH) (Heil, 2015). The commonest resource plants offer to ants is EFN, a liquid substance rich in carbohydrates with dilute concentrates of amino acids, lipids, phenols, alkaloids and volatile organic compounds (Gonzalez-Teuber and Heil, 2009). Carbohydrates have been suggested to be key resources for arboreal ants (Davidson et al., 2003).

\*Author for correspondence : E-mail: nalini\_jk@yahoo.com

Many studies have found positive net effects of EFN consumption on biocontrol organisms such as parasitoids and predatory mites, and EFN secretion represents a common trait among cultivated plants (Heil, 2015). Thus EFN-mediated defense can be well exploited in IPM programmes against a wide range of pests. Little is known about the distribution and abundance of plants with EFNs (Keeler, 1980) and very few studies have focussed on arthropod diversity at the EFNs (Rudgers, 2004), particularly of crop plants (Agarwal and Rastogi, 2010). Also more research is required to understand the importance of EFN for its consumers and, thus, for the communities of plants and arthropods in natural, disturbed, and agronomic ecosystems (Heil, 2015). With this background the present study was initiated to study the interaction between ants, other insect visitors and EFNs in selected crops.

## **Materials and Methods**

### Field incidence of ants, herbivores and predators

Field incidence of insects visiting the EFNs in selected crops viz., cotton (Gossypium hirsutum L.), black gram (Vigna mungo L. Hepper), green gram (Vigna radiata (L.), lablab (Dolichos lablab var. typicus L.), mesta (Hibiscus cannabinus L.) and castor (Ricinus communis L.) available at Annamalainagar were recorded on randomly selected 25 plants per field during October and November of 2016 (3 counts/month). The observations were made on insects number, lasting about 90 seconds at each plant on EFN-bearing plant parts. Herbivores were identified to genus level, predators to family level and ants to species level in the Department of Entomology, Faculty of Agriculture, Annamalai University (modified Agarwal and Rastogi, 2010).

### **Ant-exclusion experiment**

The protective roles of Camponotus rufoglaucus (Jerdon) and Myrmicaria brunnea Saunders against Solenopsis mealybug, Phenacoccus solenopsis Tinsely in potted Hibiscus cannabinus were tested in antexclusion experiment. Ten separate potted plants of Hibiscus cannabinus (0.86 m height) were selected for the control (with ants) and treatment (without ants). Plants of approximately the same height and in the same phenological state (no buds, flowers or fruits) were selected. Camponotus rufoglaucus and Myrmicaria brunnea were prevented from climbing on treatment plants by applying castor oil to their base a sticky barrier of plants, at weekly intervals. Also both the ants had free access to the control plants of Hibiscus cannabinus. Phenacoccus solenopsis population on control and treatment were observed weekly for one month (4 counts). The number of Camponotus rufoglaucus and Myrmicaria brunnea visiting the EFNs of control plants were counted weekly. Also predators and parasitized Phenacoccus solenopsis mummies number were recorded in both control and treatment at weekly intervals (modified Oliveira et al., 1999).

#### **Results and Discussion**

# Field incidence of ants, herbivores and predators

Observations recorded during October and November of 2016 on field incidence of insects visiting the EFNs of selected crops viz., Vigna mungo L. Hepper, Vigna radiata L., Gossypium hirsutum L., Hibiscus cannabinus L., Dolichos lablab var. typicus L. and Ricinus communis L. available at Annamalainagar are presented in Tables 1-6.

In Vigna mungo, Phenacoccus sp. population was

highest (0.25) and *Lampides* sp. population was lowest (0.10) among herbivores during October. During November also *Phenacoccus* sp. population was highest (0.48) and both *Empoasca* sp. and *Oxya* sp. population were lowest (0.20). Among predators Coccinellidae population was highest and Vespidae population was lowest during both the months. *Camponotus compressus* (3.7., 5.70) was highest in population and *Camponotus seriseus* (0.16, 0.24) was lowest during both the months (October and November) respectively among ants (Table 1).

In Vigna radiata, Coptosoma sp. population was highest (2.10) and Oxya sp. population was lowest (0.25) among herbivores during October (Table 2). During November Aphis sp. population was highest (4.52) and Oxya sp. population was lowest (0.24). Among predators Coccinellidae population was highest and Mantidae population is lowest during both the months. Amongst ants, Camponotus compressus (5.06, 7.24) was highest in population and Tetraponera nigra (0.10), Camponotus seriseus (0.37) was lowest during both the months (October, November) respectively.

In *Gossypium hirsutum*, eight species were recorded as herbivores (Table 3). Among them *Aphis* sp. population was highest (3.8, 4.29) and *Thrips* sp. population was lowest (0.20, 0.22) during both the months (October, November) respectively. Among predators Coccinellidae population was highest during both the months. Of the ants, *Camponotus compressus* (10.38, 12.31) was highest in population during both the months (October, November) respectively; *Camponotus sericeus* (0.17) was lowest during October and *Camponotus irritans* (0.65) during November.

In *Hibiscus cannabinus*, only two species were observed as herbivores among these *Phenacoccus* sp. population was highest (16.72, 19.32) and *Euproctis* sp. population was lowest (0.52, 0.43) during both the months (October, November) respectively. Among predators Coccinellidae population was highest (0.17, 0.71) and Vespidae lowest (0.16, 0.19) during both the months (October, November) respectively. *Myrmicaria brunnea* (6.36, 7.96) was highest in population; *Camponotus compressus* (0.41, 0.64) was lowest during both the months (October, November) respectively among ants (Table 4).

In *Dolichos lablab* var. *typicus*, *Helicoverpa* sp. population was highest (1.81, 1.83) and *Oxya* sp. population was lowest (0.96, 1.33) during both the months (October, November) respectively in herbivores. Among predators Vespidae population was highest, Coccinellidae

population was lowest during both the months. Of ants, *Solenopsis geminata* (6.89, 8.45) was highest in population, *Camponotus sericeus* (0.17) was lowest during both the months (October, November) respectively (Table 5).

In *Ricinus communis*, among herbivores *Aphis* sp. population was highest (1.02, 0.37) and *Oxyrachis* sp. population was lowest (0.37, 0.03) during both the months (October, November) respectively (Table 6). There were no predators during both the months. Amongst ants, *Myrmicaria brunnea* (17.19, 19.73) was highest in population; *Componotus compressus* (0.69, 1.20) was lowest during both the months (October, November) respectively.

These differences in the incidence of different ant species on different EFN crop species may be due to competitive interactions among the ant species, herbivores and other insect visitors population. Five crops *viz., Vigna mungo, Vigna radiata, Gossypium hirsutum, Dolichos lablab* var. *typicus* and *Ricinus communis* were in reproductive stage so ants as well as predators incidence were more. Thus herbivore population in these crops were reduced considerably. Ant species presence did not hinder predators activity so they too played a significant role in herbivore population reduction. But *Hibiscus cannabinus* was in vegetative stage in which ant and predator population was less than the herbivore (*Phenacoccus* sp.) population so they could not be reduced by ants and predators.

According to Agarwal and Rastogi (2010) ants occurred at particularly high relative abundance ( $84.44 \pm 4.34$  %) on EFNs. They also observed 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). This is accordance with the present findings.

Heil, *et al.*, 2004 also confirmed that ants comprised 60% of all nectary visiting arthropods at the EFN-bearing Southeast Asian myrmecophilic plant, *Macaranga tanarius*. This matches the present study results.

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 and Rastogi, 2008, 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 and Rastogi, 2008) 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 which do not deter insect pollinators and have very low deterrent effect on the insect herbivores of sponge gourd plants (Agarwal and Rastogi, 2008). 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.

This is the first study of insects associated with the EFNs of crop plants in India. The results are supported by earlier reports on the occurrence of other visitors of EFN like and ladybirds (Pemberton and Vanderberg, 1993), bees (O'Dowd, 1979), wasps (Bugg et al., 1989; Stapel et al., 1997), roaming spiders (even though mainly carnivorous: Taylor and Foster, 1996; Ruhren and Handel, 1999; Taylor and Pfannenstiel, 2008), neuropterans (Limburg and Rosenheim, 2001) and even birds (Pemberton, 1993) on the EFNs of plants. Insects representing 14 families of Diptera, 5 families of wasps (Hymenoptera), and 6 genera of ants (Hymenoptera) have been observed on the extrafioral nectaries of P. lunatus (Fabaceae) (Kost and Heil, 2005), and species in the orders Hemiptera, Diptera, Coleoptera, Hymenoptera, and Lepidoptera visit the extrafioral nectaries of Luffa cylindrica (Cucurbitaceae) Agarwal and Rastogi (2010).

#### **Ant-exclusion experiment**

Results of ant - exclusion experiment in Hibiscus cannabinus is presented in (Table 7). In control Phenacoccus solenopsis population showed gradually decreasing pattern from the first week (17.45) to fourth week (11.22). But Coccinellidae and Mantidae population showed increasing pattern during every consecutive week. Componotus rufoglaucus and Mymicaria brunnea population revealed steady increase (1.27, 2.52, 2.87 and 3.95) in population in the successive weeks. Parasitized mealybug mummies number (by the parasitoid, Aenasius arizonensis Hayat) showed decreasing pattern from (1.26-0.37) first to fourth week respectively because of the disturbance towards the parasitoid population due to both ant species by their continuous patrolling behaviour. Even though there was gradual decrease in Phenacoccus solenopsis population in consecutive weeks in control. Their population exceeded ant species

population up to second week. During third and fourth week *Mymicaria brunnea* population slowly increased even when predators population was totally nil during fourth week. Studies using different systems have reported that the consumption of EFN can enhance the aggressiveness of ants and their capacity to defend the extrafioral nectaries against potential competitors such as wasps and cheater ants (Gonzalez-Teuber *et al.*, 2012; Heil, 2013) and change the foraging preferences of ants and thus their predation behaviour (Wilder and Eubanks, 2010). This supports the present findings.

Feeding on EFN has also been reported for lady beetles (Coleoptera: Coccinellidae) such as *Coleomegilla maculata* (Lundgren and Seagraves, 2011) and *Exoplectra miniata* (Almeida *et al.*, 2011), for predatory bugs such as the assassin bug *Atopozelus opsimus* (Hemiptera, Reduviidae) (Guillermo-Ferreira *et al.*, 2012) and the omnivorous bug *Orius insidiosus* (Pumarino *et al.*, 2012), for predatory mites (Weber *et al.*, 2012), and for the mirid (Hemiptera) *Macrolophus pygmaeus* (Portillo *et al.*, 2012).

For the lady beetle *C. maculata* and the mirid *M. pygmaeus*, the authors reported an enhanced survival and fecundity in animals that had fed on EFN (Lundgren and Seagraves, 2011; Portillo *et al.*, 2012). Predatory wasps might represent a further important group of EFN consumers although, like spiders, they can be outcompeted by ants. Furthermore, the obligate myrmecophyte *Acacia hindsii* (Gonzalez-Teuber *et al.*, 2012) and the EFN-bearing plant *Banisteriopsis malifolia* (Alves-Silva *et al.*, 2013) have been reported to have higher rates of wasp visitation on extrafioral nectaries from which ants have been excluded. This is similar and confirms to the present study results.

In treatment plants (ants excluded) *Phenacoccus* solenapsis population was gradually decreasing from the first week (17.28) to fourth week (13.17). Coccinellidae and Mantidae population showed fluctuating pattern in every consecutive week with less deviation from the first week and totally nil during fourth week. Parasitized *Phenacoccus solenopsis* mummies number (by the parasitoid, *Aenasius bambawalei*) showed steady increase from first to fourth week and kept the *Phenacoccus solenopsis* population under check. This confirms ant population affects the activity of parasitoids than predators.

In both control and treatment *Phenacoccus* solenopsis population was under check but in control (11.22) their population was less when compared to treatment (13.17) during the fourth week which showed the significant role played by *Mymicaria brunnea*.

Parasitization rates of herbivores increased on EFNproducing compared with nectary free plants (Geneau *et al.*, 2013; Geneau *et al.*, 2012; Pemberton and Lee,1996; Stapel *et al.*, 1997),which might indicate that the attraction of parasitoids to extrafioral nectaries can enhance the antiherbivore defense of these plants (Hernandez *et al.*, 2013; Mathews *et al.*, 2011).

Del-Claro and Oliveira (1993) tested whether ants (Camponotus sp.) would stop tending honeydewproducing membracids (Guayaquila xiphias) when an alternative sugar source was available on the host plant (Didymopanax vinosum). Results showed that the discovery of an alternate sugar source (simulated extrafloral nectaries) did not provoke desertion by ants. Instead, tending of Guayaquila aggregations continued nearly the same as ant visitation to the honey solution increased steadily within the same period. Thus they do not support the prediction that ants would neglect honeydew-producing homopterans in the presence of extrafloral nectaries. The same observation was seen with the C. rufoglacus and Mymicaria brunnea in the present study which fed honeydew of Phenacoccus solenopsis for more time and fed nectaries of Hibiscus cannabinus for very less time which confirms EFN plants' vital role in its diet which indirectly hindered natural enemies activity.

In the last two decades, a series of experimental field studies have shown that ant visitors to EFNs can defend the plant against several types of herbivores (Bentley, 1977; Beattie, 1985; Holldobler and Wilson, 1990). This is similar to the present observation which also showed decrease of Phenacoccus solenapsis population in the presence of moderately aggressive C. rufoglaucus. Becerra and Venable (1989) proposed that EFNs may function to defend plants against ant-homoptera mutualisms by supplying ants with extrafloral nectar which would distract them from honeydew-producing homopterans. As a result of being abandoned by their tending ants, homopterans would suffer higher mortality rates (due to predation and parasitism) and their damage to the plant would be either reduced or eliminated. In short, according to Becerra and Venable (1989), "the main fitness benefit of EFN's is the reduction of homopteran damage". In a subsequent comment Fiala (1990) presented evidence against this hypothesis, and questioned the supposed superiority of extrafloral nectar to honeydew in being highly predictable in space, time and quality (as viewed by Becerra and Venable, 1989). Although it is known that ants can drop lower quality resources from their diets as higher quality ones become available, some of the studies cited by Becerra and

Month #			Не	rbivore	*			Predato	r*	Ant species*					
	Oxya sp.	Riptortus sp.	Lampides sp.	Empoasca sp.	Phenacoccus sp.	Oxyrachis sp.	Coccinellidae	Mantidae	Vespidae	Camponotus compressus	Camponotus irritans	Camponotus rufoglaucus	Camponotus sericeus	Solenopsis geminata	Tetraponera nigra
October 2016	0.12	0.22	0.10	0.13	0.25	0.20	0.38	0.08	0.05	3.70	0.70	2.12	0.16	1.88	0.90
November2016	0.20	0.32	0.25	0.20	0.48	0.45	0.75	0.17	0.26	5.70	2.68	3.64	0.24	2.69	1.78

Table 1: Field incidence of ants, herbivores and predators in Vigna mungo.

\* Mean of twenty five plants.

# Mean of three counts.

Table 2: Field incidence of ants, herbivores and predators in Vigna radiata.

Month #			Herb	ivore*		Pred	ator*	Ant species*						
	Oxya sp.	Coptosoma sp.	Lampides sp.	Empoasca sp.	Aphis sp.	Coccinellidae	Mantidae	Camponotus compressus	Camponotus irritans	Camponotus rufoglaucus	Camponotus sericeus	Myrmicaria brunnea	Tetraponera nigra	
October2016	0.25	2.10	0.60	0.64	0.39	1.30	0.17	5.06	1.16	1.32	0.16	0.76	0.10	
November2016	0.24	3.10	1.02	0.72	4.52	1.29	0.21	7.24	2.37	2.51	0.37	0.81	2.10	

\* Mean of twenty five plants.

# Mean of three counts.

Table 3: Field incidence of ants, herbivores and predators in Gossypium hirsutum.

Month #	Herbivore*								Predator*				Ant species*				
	Dysdercus sp.	Atractomorpha sp.	Phenacoccus sp.	Aphis sp.	Bemisia sp.	Oxyrachis sp.	Thrips sp.	Amrasca sp.	Coccinellidae	Mantidae	Vespidae	Libellulidae	Camponotus compressus	Camponotus rufoglaucus	Camponotus sericeus	ti o	Myrmicaria hrunnea
October 2016	1.15	0.24	2.50	3.80	0.38	0.92	0.20	0.40	0.80	0.17	0.14	0.13	10.38	2.39	0.17	0.24	4.12
November 2016	1.57	0.57	2.79	4.29	0.59	1.00	0.22	0.42	0.81	1.32	0.13	0.15	12.31	4.68	0.67	0.65	4.17

\* Mean of twenty five plants.

# Mean of three counts.

Table 4: Field incidence of ants, herbivores and predators in *Hibiscus cannabinus*.

Month #	Herb	ivore*		Predator	*	Ant species*			
	Phenacoccus sp.	Euproctis sp.	Coccinellidae	Mantidae	Vespidae	Camponotus compressus	Camponotus rufoglaucus	Myrmicaria brunnea	
October 2016	16.72	0.52	0.17	0.29	0.16	0.41	5.04	6.36	
November 2016	19.32	0.43	0.71	0.34	0.19	0.64	7.80	7.96	

\* Mean of twenty five plants.

# Mean of three counts.

#### T. Nalini and R. Jayanthi

Month#		Herbivore	*		Predator '	•	Ant species*						
	Oxya sp.	Riptortus sp.	Helicoverpa sp.	Coccinellidae	Mantidae	Vespidae	Camponotus compressus	Camponotus rufoglaucus	Camponotus sericeus	Tetraponera nigra	Solenopsis geminata		
October 2016	0.96	1.64	1.81	0.13	0.25	0.80	3.73	4.76	0.24	0.96	6.89		
November 2016	1.33	1.61	1.83	0.24	0.27	0.83	3.75	6.37	0.64	1.77	8.45		

Table 5: Field incidence of ants, herbivores and predators in Dolichos lablab var. typicus.

\* Mean of twenty five plants.

# Mean of three counts.

Table 6: Field incidence of ants, herbivores and predators in Ricinus communis.

Month #	Nonth # Herbivore*						Ant species*					
	Empoasca sp.	Bemisia sp.	Oxyrachis sp.	Aphis sp.	Coccinellidae	Mantidae	Camponotus compressus	Camponotus rufoglaucus	Myrmicaria brunnea	Monomorium scabriceps		
October 2016	0.68	0.47	0.37	1.02	0.00	0.00	0.69	1.48	17.19	7.34		
November 2016	1.36	0.44	0.03	1.80	0.00	0.00	1.20	2.60	19.73	8.88		

\* Mean of twenty five plants.

# Mean of three counts.

Table 7: Influence of ant- exclusion on the incidence of mealybug and its natural enemies in *Hibiscus cannabinus*.

		Contro	l (With a	nts)			-	Freatment	(Ants e	xcluded)
Week		Pred	lator*	Ant species*				Pred	ator*	
	Phenacoccus solenopsis *	Coccinellidae	Mantidae	Camponotus rufoglaucus	Myrmicaria brunnea	Parasitized Phenacoccus solenopsis *	Phenacoccus solenopsis *	Coccinellidae	Mantidae	Parasitized Phenacoccus solenopsis *
First	17.45	0.30	0.27	1.27	2.45	1.26	17.28	1.27	0.85	1.97
Second	16.92	1.00	0.58	2.52	9.65	1.22	17.70	1.45	1.02	1.27
Third	13.27	1.18	0.92	2.57	14.40	0.90	14.60	1.25	0.80	1.30
Fourth	11.22	-	-	3.95	13.12	0.37	13.17	-	-	2.17

\* Mean of ten plants.

Venable (1989) in support of the "ant-distraction hypothesis" either do not corroborate it, or actually show the opposite (Addicott, 1978, 1979; Sudd and Sudd, 1985). In fact, existing information suggest that ants switch from visiting a plant's EFN to visiting honeydew-producing homopterans (Buckley, 1983; Sudd and Sudd, 1985; Way, 1954). Becerra and Venable (1989, 1991) suggested that well designed experiments were needed before a firm conclusion on the subject could be drawn. More recently, Rashbrook *et al.* (1992) experimentally showed that the foliar nectaries of bracken fern do not reduce tending levels of homopterans, and ants strongly prefer homopteran honeydew to foliar nectar. This is similar to the present findings in which both the *C. rufoglacus* and

*Mymicaria brunnea* showed preference to homopteran (*Phenacoccus solenapsis*) honeydew more than *Hibiscus cannabinus* nectaries.

Some ants track seasonal and diurnal changes in extrafloral nectar production (Tilman, 1978; Stephenson, 1982; Gaume and McKey, 1999), exhibit preferences for nectars or honeydews on the basis of sugar and/or amino acid composition (Lanza, *et al.*, 1993; Volkl *et al.*, 1999), and stay longer in patches with more sugar (Bonser *et al.*, 1998). Similarly, nectar-satiated parasitoids stay in herbivore-occupied patches longer and attack more herbivores (Stapel *et al.*, 1997). These observations suggest that plants with increased nectar production could attract or retain more bodyguards, thereby receiving

greater protection against herbivores. This supports the present study results.

The secretion of EFN is one of the taxonomically most widespread strategies for plant defence against herbivores and one of the few traits for which metaanalyses regularly find net defensive effects. The spatiotemporal patterns in EFN secretion appear to be adapted for an optimized defence, although simple physiological mechanisms are likely to underlie at least a part of these patterns. A wide variety of predatory and parasitoid arthropods can gain a significant energy supply from feeding on EFN, and many of these are important keystone species that can affect further species in their respective ecosystems. Thus, it is likely that EFN secretion has multiple effects at the level of entire ecosystems (Heil, 2015).

EFN is cheap to produce, is naturally produced by many cultivated species, and provides direct benefits to multiple beneficial insects. A major shortcoming might be that contemporary agricultural ecosystems do not provide stable populations of, for example, natural parasitoids or ants or other predators. Planting field margins with EFN bearing species might be a promising avenue to explore (Geneau *et al.*, 2012; Olson and Wackers, 2007). Similarly, the active release of beneficial arthropods in combination with planting EFN-producing crops, or intercropping with EFN-secreting species, provides interesting perspectives (Orre-Gordon *et al.*, 2013). Thus, EFN could keep the biocontrol agents at stable population levels within the agricultural field even during pest-free periods.

In precise, systematic descriptive and experimental surveys are required to understand the effects of EFN secretion on food webs and its positive effects on ants and the resulting cost for the EFN-secreting plants. Also in future attempts should be made to understand the role of EFN in the structuring of arthropod communities and it is necessary to integrate EFN into different types of biocontrol programmes for efficient pest management.

# References

- Addicott, J.F. (1978). The population dynamics of aphids on fireweed: a comparison of local and metapopulations. *Canadian Journal of Zoology*, 56: 2554 2564.
- Addicott, J.F. (1979). A multispecies aphid ant association: density dependence and species specific effects. *Canadian Journal of Zoology*, **57:** 558-569.
- Agarwal, V.M. and N. Rastogi (2008). Deterrent effect of a guild of extrafloral nectary-visiting ant species on *Raphidopalpa foveicollis*, a major insect pest of sponge gourd, *Luffa cylindrica*. *Entomolgia Experimentalis et*

Applicata, 128: 303–11.

- Agarwal, V.M. and N. Rastogi (2009). Food resource and temporal partitioning amongst a guild of predatory agroecosystem-inhabiting ant species. *Current Zoology*, **55(5)**. In press
- Agarwal, V.M. and N. Rastogi (2010). Ants as dominant insect visitors of the extrafloral nectaries sponge gourd plant, *Luffa cylindrica* (L) (Cucurbitaceae). *Asian Myrmecology*, 3: 45-54.
- Agarwal, V.M., N. Rastogi and S.V.S. Raju (2007). Impact of predatory ants on two lepidopteran insect pests in Indian cauliflower agroecosystems. *Journal of Applied Entomology*, **131:** 493–500.
- Almeida, L.M., G.H. Correa, J.A. Giorgi and P.C. Grossi (2011). New record of predatory ladybird beetle (Coleoptera, Coccinellidae) feeding on extrafioral nectaries. *Revista Brasileria de Entomologia*, 55: 447–50.
- Alves-Silva, E., GJ. Baronio, H.M. Torezan-Silingardi and K. Del-Claro (2013). Foraging behavior of *Brachygastra lecheguana* (Hymenoptera: Vespidae) on *Banisteriopsis malifolia* (Malpighiaceae): extrafloral nectar consumption and herbivore predation in a tending ant system. *Entomological Science*, **16**: 162–69.
- Beattie, A.J. (1985). The Evolutionary Ecology of Ant– plant Mutualisms. Cambridge: Cambridge University Press, 89.
- Becerra, J.X. and D.L. Venable (1989). Extrafloral nectaries: a defense against ant-Homoptera mutualisms? *Oikos*, **55**: 276-280.
- Becerra, J.X. and D.L. Venable (1991). The role of ant–Homoptera mutualisms in the evolution of extrafloral nectaries. *Oikos*, **60**: 105–106.
- Bentley, B.L. (1977). Extra-floral nectaries and protection by pugna-cious bodyguards. *Annual Review of Ecology and Systamatics*, **8:** 407–427.
- Bonser, R., P.J. Wright, S. Bament and U.O. Chukwu (1998). Optimal patch use by foraging workers of *Lasius* fuliginosus, L. niger and Myrmica ruginodis. Ecological Entomology, 23: 15–21
- Buckley, R.C. (1983). Interaction between ants and membracid bugs decreases growth and seed set of host plant bearing extrafloral nectaries. *Oecologia*, **58**: 132-136.
- Bugg, R.L., R.T. Ellis and R.W. Carlson (1989). Ichneumonidae (Hymenoptera) using extrafloral nectar of faba bean (Vicia faba L, Fabaceae) in Massachusetts. Biological Agriculture and Horticulture, 6: 107–14.
- Davidson, D.W., S.C. Cook, R.R. Snelling and T.H. Chua (2003). Explaining the abundance of ants in lowland tropical rainforest canopies. *Science*, **300**: 969-72.
- Del-Claro, K. and P.S. Oliveira (1993). Ant-Homoptera interaction: do alternative sugar sources distract tending ants? Oikos, 68: 202–206.
- extrafloral nectaries as a source of ecological costs of an indirect defence. *Journal of Tropical Ecology*, **20:** 1–8.

- Fiala, B. (1990). Extrafloral nectaries versus ant–Homoptera mutualism: a comment on Becerra and Venable. *Oikos*, 59: 281–282.
- Gaume, L. and D.B. McKey (1999). An ant-plant mutualism and its host-specific parasite: activity rhythms, young leaf patrolling, and effects on herbivores of two specialist plantants inhabiting the same myrmecophyte. *Oikos*, **84:** 130– 144.
- Geneau, C.E., F.L. Wackers, H. Luka and O. Balmer (2013). Effects of extrafioral and fioral nectar of *Centaurea cyanus* on the parasitoid wasp *Microplitis mediator*: olfactory attractiveness and parasitization rates. *Biological Control*, **66**: 16–20.
- Geneau, C.E., F.L. Wackers, H. Luka, C. Daniel and O. Balmer (2012). Selective fiowers to enhance biological control of cabbage pests by parasitoids. *Basic Applied Ecolology*, 13: 85–93.
- Gonzalez-Teuber, M. and M. Heil (2009). The role of extrafloral nectar amino acids for the preferences of facultative and obligate ant mutualists. *Journal of Chemical Ecology*, 35: 459–68.
- Gonzalez-Teuber, M., J.C. Silva Bueno, W. Boland and M. Heil (2012). Increased host investment in extrafioral nectar (EFN) improves the efficiency of a mutualistic defensive service. *Plos one*, **7**: e 46598.
- Guillermo-Ferreira, R., R. Cardoso-Leite and R. Gandolfo (2012). First observation of alternative food usage (extrafioral nectar) by the assassin bug *Atopozelus opsimus* (Hemiptera,Reduviidae). *Revista Brasiliian Entomologyst*, 56: 489–91.
- Heil, M. (2013). Let the best one stay: Screening of ant defenders by Acacia host plants functions independently of partner choice or host sanctions. *Journal of Ecology*, **101:** 684–88.
- Heil, M. (2015). Plant- insect interface: A spotlight on chemical Ecology, phenotype Plasticity, and Food webs. *Annual Review of Entomology*, **60**: 213-32.
- Heil, M., A. Hilpert, R. Kruger and K.E. Linsenmair (2004). Competition among visitors to
- Hernandez, L.M., J. Tupac Otero and M.R. Manzano (2013). Biological control of the greenhouse whitefiy by *Amitus fuscipennis*: understanding the role of extrafioral nectaries from crop and non-crop vegetation. *Biological Control*, **67**: 227–34.
- Holldobler, B. and E.O. Wilson (1990). The ants. Harvard University Press. Nature, 732.
- Keeler, K.H. (1980). Distribution of extrafloral nectaries in temperate communities. *American Midland Naturalist*, 104: 274-280.
- Kost, C. and M. Heil (2005). Increased availability of extrafioral nectar reduces herbivory in lima bean plants (*Phaseolus lunatus*, Fabaceae). *Basic Applied Ecology*, 6: 237–48.
- Lanza, J., E.L. Vargo, L. Pulim and Y.Z. Chang (1993). Preferences

of the fire ants *Solenopsis invicta* and *S. geminata* (Hymenoptera: Formicidae) for amino acid and sugar components of extrafloral nectars. *Environmental Entomology*, **22**: 411-417.

- Limburg, D.D. and J.A. Rosenheim (2001). Extrafloral nectar consumption and its influence on survival and development of an omnivorous predator, larval *Chrysoperla plorabunda* (Neuroptera: Chrysopidae). *Environmental Entomology*, **30**: 595–604.
- Lundgren, J.G. and M.P. Seagraves (2011). Physiological benefits of nectar feeding by a predatory beetle. *Biological Journal of the Linnean Society*, **104:** 661–69.
- Mathews, C.R., D.G. Bottrell and M.W. Brown (2011). Interactions between extrafioral nectaries, ants (Hymenoptera: Formicidae), and other natural enemies affect biological control of *Grapholita molesta* (Lepidoptera: Tortricidae) on peach (Rosales:Rosaceae). *Environmental Entomology*, **40**: 42–51.
- O'Dowd, D.J. (1979). Foliar nectar production and ant activity on a neotropical tree. *Ochrorna pyramidale*. *Oecologia* (*Berlin*), **43**: 233–48.
- Oliveira, P.S., V. Rico-Gray, C. Diaz-Castelazo and C. Castillo-Guevara (1999). Interaction between ants, extrafloral nectaries and insect herbivores in Neotropical coastal sand dunes: herbivore deterrence by visiting ants increases fruit set in *Opuntia stricta* (Cactaceae). *Functional Ecology*, **13**: 623–31.
- Olson, D.M. and F.L. Wackers (2007). Management of field margins to maximize multiple ecological services. *Journal* of Applied Ecology, **44:** 13–21.
- Orre-Gordon, G, S.D. Wratten, M. Jonsson, M. Simpson and R. Hale (2013). 'Attractandreward': combining herbivoreinduced plant volatile with floral resource supplementation-multi-trophic level effects. *Biological Control*, **64**: 106–15.
- Pemberton, R.W. and N. J. Vandenberg (1993). Extrafloral nectar feeding by ladybird beetles (Coleoptera: Coccinellidae). *Proceedings of the Entomological Society of Washington*, **95:** 139–151.
- Pemberton, RW. (1993). Observations of extrafloral nectar feeding by predaceous and fun- givorous mites. Proceedings of the Entomological Society. *Wash*, 95: 642-645.
- Pemberton, R.W. and J.H. Lee (1996). The influence of extrafioral nectaries on parasitism of an insect herbivore. *American Journal of Botany*, 83: 1187–94.
- Portillo, N., O. Alomar and F. Wackers (2012). Nectarivory by the plant-tissue feeding predator *Macrolophus pygmaeus* Rambur (Heteroptera:Miridae):nutritional redundancy or nutritional benefit? *Journal of Insect Physiolgy*, **58:** 397– 401.
- Pumarino, L., O. Alomar and J.G. Lundgren (2012). Effects of floral and extrafloral resource diversity on the fitness of an omnivorous bug, Orius insidiosus. *Entomologia*

Interaction between ants, other insect visitors and extrafioral nectaries (EFNs) in selected crops from India 2113

Experimentalis et Applicata., 145:181–90.

- Rashbrook, V.K., S.G. Compton and J.H. Lawton (1992). Ant– herbivore interactions- reasons for the absence of benefits to a fern with foliar nectaries. *Ecology*, **73**: 2167–2174.
- Rudger, J.A. (2004). Enemies of herbivore can shape plant trait: selection in a facultative ant- plant mutualism. *Ecology*, 85 (1): 192-205.
- Ruhren, S. and S.N. Handel (1999). Jumping spiders (Salticidae) enhance the seed production of a plant with extrafloral nectaries. *Oecologia*, **119**: 227–230.
- Stapel, J.O., A.M. Cortesero, C.M. DeMoraes, J.H. Tumlinson and W.J. Lewis (1997). Extrafioral nectar, honeydew, and sucrose effects on searching behavior and efficiency of *Microplitis croceipes* (Hymenoptera:Braconidae) in cotton. *Environmental Entomology*, 26: 617–23.
- Stephenson, A.G. (1982). Iridoid glycosides in the nectar of *Catalpa speciosa* are unpalatable to nectar thieves. *Journal of Chemical Ecology*, 8(7): 1025–34.
- Sudd, J.H. and M.E. Sudd (1985). Seasonal changes in the response of wood-ants (*Formica lugubris*) to sucrose baits. *Ecological Entomology*, **10**: 89–97.

Taylor, R.M. and W.A. Foster (1996). Spider nectarivory.

American Entomologist, 42: 82–86.

- Taylor, R.M. and R.S. Pfannenstiel (2008). Nectar feeding by wandering spiders on cotton plants. *Environmental Entomology*, 37(4): 996–1002.
- Tilman, D. (1978). Cherries, ants and tent caterpillars: timing of nectar production in relation to susceptibility of caterpillars to ant predation. *Ecology*, **59**: 686-692.
- Volkl, W., J. Woodring, M. Fischer, M.W. Lorenz and K.H. Hoffman (1999). Ant-aphid mutualisms: the impact of honeydew production and honeydew sugar composition on ant preferences. *Oecologia*, **118**: 483–491.
- Way, M.J. (1954). Studies on the association of the ant Oecophylla longinoda (Lat.) with the scale insect Saisseria zanzibarensis Williams (Coccoidae). Bulletin of Entomological Research, 45: 113-134.
- Weber, M.G., W.L. Clement, M.J. Donoghue and A.A. Agrawal (2012). Phylogenetic and experimental tests of interactions among mutualistic plant defense traits in Viburnum (Adoxaceae). *American Naturalist*, **180**: 450–63.
- Wilder, S.M. and M.D. Eubanks (2010). Extraforal nectar content alters foraging preferences of a predatory ant. *Biology Letters*, **6**: 177–79.