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Leafhopper food plants in a Neotropical forest in Panama (Hemiptera: Cicadellidae)

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Abstract: The leafhoppers (Cicadellidae) are a group of insects that suck sap from vascular plants. The host plants of most species of Cicadellidae are unknown, but some species are known to have a wide range of food plants, while others are host plant specific. The aim of this study was to record the food and host plants for leafhoppers in a Neotropical rainforest. The study area was located in the lowland forests of Panama Province (Central Panama) in two National Parks. Sampling was done in the undergrowth, canopy and emergent strata to collect the cicadellids feeding on the trees, shrubs, seedlings, and vines there. We collected 118 cicadellid adult representing 24 species, 21 genera, and six subfamilies, which fed on 49 species of plants, belonging to 31 families. The subfamily with the largest number of species was the Cicadellinae with 11, while the plant family with the most species was the Fabaceae with five species, and the favorite plant was *Anacardium excelsum,* which hosted six cicadellid species and 10 individuals. According to estimates by Shannon Weiner, leafhopper communities are more diverse on trees than on shrubs, vines, or grasses.

Key words: Food plants, host plants, polyphagous, leafhoppers, feeding.

INTRODUCTION

For most species of leafhoppers (Cicadellidae), host plants are unknown (Freytag & Sharkey 2002). Among those for which host plants are known, some species have a wide range of food plants while others are host specific, and usually they are restricted to definite plant species or genera (Lamp et al. 1994). In turn, the plants are limited to definite habitats largely due to climatic and edaphic conditions (DeLong 1948).

Most studies on the relationships between Cicadellidae and plants have focused on pests that attack economically important plants (Poos & Wheeler 1943, DeLong 1948, Purcell 1976, Zanol & de Menezes 1982), distribution of eggs on plant species (Miller & Hibbs 1963), plant species tested as alternate hosts (Claridge et al. 1977), leafhoppers that alternate between hosts (Claridge & Wilson 1978). Many Cicadellidae have been reared in captivity to analyze their associations with potential plant hosts, and their life cycles, oviposition, content of amino acid in xylem and feeding behavior (Ståhl 1920, Swain 1936, Palmiter et al. 1960, Saxena & Saxena 1974, Stiling 1980, Brodbeck et al. 1993).

Some studies have been conducted on the relationships between wild host plants (grasses) and Cicadellidae in northern temperate areas (Prestidge & McNeil 1983, Whitcomb et al. 1987, Novotný 1995, Eyre et al. 2001). Brown et al. (1992) compared leafhoppers with matched grassland to see the effect of foodplant architecture and species composition of leafhoppers. Hamilton (1994), studied the evidence for leafhopper origins in Northeastern relict prairies (USA and Canada). Dietrich (1999, 2013) did a phylogenetic analysis of some leafhopper taxa to assess the

role of grassland on leafhopper diversification. Biedermann et al. (2005), Hollier et al. (2005), Nickel & Achtziger (2005) studied the leafhoppers from grasslands in Germany, as indicators of habitat condition and restoration. Other studies have been done in temperate zones of South America such as Virla et al. (2008), and Paradell et al. (2012), who found associations between Proconiini (Cicadellinae) and host plants.

In tropical regions some studies have been done on Cicadellidae to learn their host plants (Lozada 1993, Bennett & O'Grady 2011, Bennett & O'Grady 2012) or their relationships with seedlings (Basset 2000), or strata such as, canopy (Montgomery & Lubin 1979 as reported by Wolda 1979, Nadkarni & Longino 1990, Kishimoto-Yamada et al. 2015), or undergrowth (Novotný & Leps 1997). Other studies included introduced leafhoppers (Jones et al. 2000) and oviposition of two invasive leafhopper species on an endemic tree (Alyokhin et al. 2004).

Other studies included Cicadellidae as a minor contribution: Basset (2001) did a review of papers on invertebrates in the tropical rainforest canopy. Novotný et al. (2012), in New Guinea, studied the low diversity within specialist herbivore guilds. The objective of our study was to record the species of food and host plants from leafhoppers in a tropical rainforest of Panama, due to the importance of knowing their associations with tropical forest plants species. According to Poos & Wheeler (1943), a host plant is a plant from which leafhoppers have been reared, and a food plant is one upon which adults were only collected feeding or probing.

MATERIALS AND METHODS

Study area and food plants

The study area was situated in the lowland forests of Panama Province (Central Panama), in two National Parks. In the first, the Parque Natural Metropolitano (PNM) (8°59'45.93''N, 79°32'38.08''OW, 30 m asl) comprises an area of 270 ha, in the city of Panama, Province of Panama. The PNM joins the Parque Camino de Cruces and the Parque Nacional Soberania in the Biological Corridor along the eastern coast of Panama (Viquez & Denvers 2006). The park is located in the transition zone between the tropical dry and humid forests, and therefore consists of a mixture of these two biomes. This protected area is one of the last refuges of the threatened Pacific Dry Tropical Forest in Central America (Parque Natural Metropolitano 2008). The other study area is very close to PNM and is the dry forest that borders the campus of the Universidad Tecnologica de Panama (UTP). We did observations in three forest layers, undergrowth, canopy (PNM) and emergent (PNM).

The second park was the Parque Nacional Soberania (PNS), which is about 30 minutes from the city. It is a tropical rainforest (9°01'24''N, 79°32'08''W, 64 m asl), and in it we had two study areas: El Charco trail (9° 4'56.13"N, 79°39'53.58"W) and Plantation Road (9°4'51.08"N, 79°39'7.10"W, ca= 154 m asl). In both only the undergrowth was investigated.

Sampling of leafhoppers

The undergrowth (0 – 4 m) was investigated by walking along trails. Trees and vines of the canopy (5 - 30 m) and emergent levels (31 - 40 m) were searched from a canopy crane operated by the Smithsonian Tropical Research Institute (STRI). The canopy crane consists of a gondola connected to a tower crane. Access to all levels of the forest canopy is carried out from the gondola. The crane is 42 m tall and has a 51 m horizontal boom. The crane facilitates the study of approximately 8,000 m^2 and 200,000 m^3 of forest (Wright & Colley 1994).

From March-April 2013 to August 2013 and June-August 2015, we did the sampling by walking inside the forest to observe the behavior of leafhoppers on different parts of plants including leaf surfaces, branches, and flowers. Live insects were collected by hand using vials and sweep nets. We recorded whether there were immature stages to determine whether this species of plant was their host plant.

All observations in the undergrowth were made from 30 cm to 1.7 m of from the ground. Each collected specimen and its food or host plant were given the same number. Plants were marked with masking tape. If more than one specimen was collected on the same plant, they all got the same number referring to the plant they were feeding and collected on. Even if the leafhoppers moved to a different plant during collection, the first observed plant was considered to be the food plant. We use the criterion of host plants and food plants from Poos & Wheeler (1943), host plant is the plant from which a leafhopper has been reared and food plant is one upon which adults were only collected feeding or probing.

Preparation of the leafhoppers and plants

In the laboratory, all the leafhoppers were frozen for at least 30 minutes and then mounted on points on entomological pins. The collected plants were pressed, identified and mounted to compare and determine at the Herbario de la Universidad de Panamá. Species names of described leafhoppers were obtained by comparing them with specimens in the Insect Collection from STRI and with published papers on leafhopper taxonomy, and were determined by Edwin Dominguez, expert taxonomist. All leafhopper specimens and their food plants were listed in an Excel database.

Data analysis

Species diversity of insects and their food plants was calculated using three measures: dominance of species, Shannon-Wiener information, and Simpson diversity, to make comparisons among population's Cicadellidae in plant forms (habitus): trees, shrubs, vines, and grasses. The diversity index was calculated using the software Past version 2.16 (Hammer et al. 2001), a free statistical software package.

Simpson Index. reflects the probability of two individuals randomly selected belonging to the same species. It varies from 0 to 1 and the higher the probability of individuals representing the same species, that is, the greater the dominance and lower the diversity.

Shannon-Wiener Index. It measures the degree of uncertainty in which species will belong to a chosen individual, at random, of a sample with species and individuals. Usually this index is between 1.5 and 3.5, rarely exceeding 4.5. The lower the value of the Shannon index, the lower the uncertainty and, therefore, the lower the sample diversity. Diversity tends to be higher as the value of the index increases.

Equitability (J') varies between 0 and 1, values greater than 0.5, being considered indicative of uniformity in the distribution of the species in the place studied.

We used a principal component analysis (PCA) to analyze the relationship between leafhopper species associated to plant habitus. The PCA was calculated using the software Past version 2.16.

RESULTS

We collected 118 adult specimens representing 24 species of Cicadellidae, 21 genera, and six subfamilies (Table I), which fed on 49 species of plants, belonging to 31 families.

Table I. Food plants recorded of Cicadellidae species from Central Panama.

Cicadellidae Subfamily	Cicadellidae species	Food plant species	Habitus	Strata	Locality	No. specim. per plant species
Arecaceae						
Cicadellinae	*Ladoffa ignota*	*Desmoncus orthacanthos* Mart.	**V**	U	PNM	10
Cicadellinae	*Soosiulus salutaris*			U	El Charco	1
Anacardiaceae						
Cicadellinae	*Soosiulus salutaris*	*Anacardium excelsum* (Bertero & Balb. ex Kunth) Skeels	**T**	E	Plantation Road	1
Cicadellinae	*Acrogonia nigriceps*			E/C	PNM	4
Cicadellinae	*Nielsonia sp.*			E/C	PNM	1
Cicadellinae	*Acrogonia obscurior*			E	PNM	2
Coelidiinae	*Coelidia sp.*			E	PNM	1
Cicadellinae	*Graphocephala riverae*			C	PNM	1
Annonaceae						
Typhlocybinae	*Joruma sp.*	*Annona spraguei* Saff.	T	U	PNM	1
Apocynaceae						
Cicadellinae	*Soosiulus salutaris*	*Rauvolfia littoralis* Rusby	T	U	El Charco	2
Bignoniaceae						
Cicadellinae	*Ladoffa ignota*	*cf. Arrabidae*	V	U	PNM	1
Cicadellinae	*Ladoffa ignota*	*Tabebuia guayacan* (Seem.) Hemsl.	T	U	PNM	1
Cicadellinae	*Ladoffa sanionis*	Bignoniaceae sp.	T	U	PNM	1
Cicadellinae	*Soosiulus salutaris*			U	El Charco	2
Convolvulaceae						
Cicadellinae	*Graphocephala riverae*	*Bonamia trichanta* Hallier f.	V	C	PNM	3
Cucurbitaceae						
Cicadellinae	*Ladoffa ignota*	Psiguria sp.	V	U	PNM	1
Elaeocarpaceae						
Idiocerinae	*Bolivianoscopus sp.*	*Sloanea terniflora (Sessé & Moç. ex DC.) Standl.*	T	U	PNM	1
Cicadellinae	*Ladoffa ignota*			U	PNM	1
Euphorbiaceae						
Cicadellinae	*Baleja rufofasciata*	*Acalypha diversifolia* Jacq.	S	U	El Charco	1
Fabaceae-Caesalpinioide						

Table I. Continuation.

Cicadellinae	*Ladoffa ignota*	*Senna papillosa* (Britton & Rose) H.S. Irwin & Barneby *var. Papillosa*	S	U	PNM	1
Fabaceae-Mimosoideae						
Cicadellinae	*Egidemia paranceps*	*Cojoba rufescens* (Benth.) Britton & Rose	T	U	UTP	1
Cicadellinae	*Graphocephala riverae*	*Inga alba* (Sw.) Willd.	T	U	UP	1
Agallinae	*Agalliopsis imitans*	*Inga sapindoides* Willd.	T	U	PNM	1
Cicadellinae	*Stephanolla cazapana*	*Inga* sp.	T	U	Plantation Road	1
Cicadellinae	*Ladoffa ignota*	Fabaceae sp.	T	U	Plantation Road	1
Heliconiaceae						
Cicadellinae	*Beirneola anita*	*Heliconia latispatha* Benth.	G	U	UTP	1
Cicadellinae	*Ladoffa ignota*			U	PNM	2
Lecythidaceae						
Cicadellinae	*Soosiulus salutaris*	*Gustavia superba* (Kunth) O. Berg	T	U	Plantation Road	1
Loganiaceae						
Cicadellinae	*Soosiulus salutaris*	*Strychnos panamensis* Seem.	V	U	El Charco	1
Malpighiacea						
Cicadellinae	*Soosiulus salutaris*	*Hiraea* sp.	V	U	El Charco	1
Gyponinae	*Gypona arunda*	Malpighiaceae sp.	V	U	PNM	2
Cicadellinae	*Ladoffa ignota*			U	PNM	1
Malvaceae						
Typhlocybinae	*Empoasca alceda*	*Luehea seemannii* Triana & Planch.	T	C	PNM	3
Melastomataceae						
Coelidiinae	*Licontinia introducens*	*Miconia argentea* (Sw.)DC.	S	U	Cerro Ancón	1
Meliaceae						
Cicadellinae	*Soosiulus salutaris*	*Guarea guidonia* (L.) Sleumer	T	U	El Charco	1
Cicadellinae	*Soosiulus salutaris*	*Protium glabrum* (Rose) Engl.	T	U	El Charco	2
Cicadellinae	*Ladoffa ignota*	*Azadirachta indica* A. Juss.	T	U	UTP	1
Moraceae						

Table I. Continuation.

Gyponinae	*Gypona arunda*	*Castilla elastica* Sessé ex Cerv. var. *costaricana* (Liebm.) C.C. Berg	T	C	PNM	1
Typhlocybinae	*Empoasca alceda*			C	PNM	12
Cicadellinae	*Acrogonia nigriceps*			E	PNM	1
Cicadellinae	*Nielsonia sp.*	*Ficus insipida* Willd.	T	E	PNM	2
Cicadellinae	*Acrogonia nigriceps*			E	PNM	6
Cicadellinae	*Soosiulus salutaris*	*Sorocea affinis* Hemsl.	T	U	El Charco	5
Cicadellinae	*Stephanolla cazapana*			U	Plantation Road	1
Myrsinaceae						
Cicadellinae	*Soosiulus salutaris*	*Stylogyne turbacensis (Kunth) Mez subsp. laevis (Oerst.) Ricketson & Pipoly*	S	U	El Charco	1
Ochnaceae						
Idiocerinae	*Luteobalmus sp.*	*Ouratea lucens* (Kunth) Engl.	S	U	PNM	1
Piperaceae						
Cicadellinae	*Stephanolla cazapana*	*Piper colonense C. DC.*	S	U	UTP	1
Cicadellinae	*Ladoffa ignota*			U	UTP	1
Cicadellinae	*Ladoffa ignota*	*Piper reticulatum* L.	S	U	PNM	2
Agallinae	*Agalliopsis imitans*	*Piper umbellatum L.*	S	U	El Charco	6
Poaceae						
Cicadellinae	*Apogonalia fractinota*	*Chusquea sp.*	G	U	UTP	1
Polygonaceae						
Cicadellinae	*Soosiulus salutaris*	*Coccoloba manzinellensis Beurl.*	T	U	El Charco	1
Rubiaceae						
Coelidiinae	*Docalidia mcintoshi*	*Calycophyllum candidissimum* (Vahl) DC.	T	U	UTP	1
Cicadellinae	*Ladoffa ignota*			U	PNM	2
Cicadellinae	*Ladoffa ignota*	*Faramea sp.*	S	U	UTP	1
Cicadellinae	*Acrogonia nigriceps*	*Pittoniotis trichantha Griseb*	T	C	PNM	1
Cicadellinae	*Apogonalia fractinota*	*Psychotria sp.*	S	U	UTP	1
Rutaceae						
Cicadellinae	*Soosiulus salutaris*	*Citrus sinensis*	S	U	El Charco	1
		Salicaceae				

Table I. Continuation.

Gyponinae	*Gypona blantoni*	*Casearia arborea (Rich.) Urb.*	T	U	El Charco	0
Sapindaceae						
Coelidiinae	*Licontinia introducens*	*Matayba glaberrima Radlk.*	S	U	Cerro Ancón	1
Sapotaceae						
Cicadellinae	*Homalodisca indefensa*	*Chrysophyllum cainito L.*	T	E	PNM	2
Siparunaceae						
Gyponinae	*Gypona arunda*	*Siparuna cf. pauciflora* (Beurl.) A. DC.	S	U	PNM	1
Sterculiaceae						
Cicadellinae	*Ladoffa ignota*	*Herrania purpurea* (Pittier) R.E. Schult.	T	U	Plantation Road	1
Tectariaceae						
Cicadellinae	*Soosiulus salutaris*	*Tectaria incisa* Cav.	F	U	El Charco	1
Cicadellinae	*Soosiulus salutaris*	*Tectaria mexicana* (Fée) C.V. Morton	F	U	El Charco	2
Coelidiinae	*Pilosana gratiosa*			U	El Charco	1
Total individual						**118**

T= Tree, V= Vine, S= Shrub, F= Fern, G= Grass, U= Undergrowth, C= Canopy, E= Emergent.

Of the species found in our study, 67% were singletons (16 species). Some species were polyphagous such as *Ladoffa ignota* (n = 25) and *Soosiulus salutaris* (n = 22) that fed on 13 and 15 plant species each. Other species fed on four species of food plants: *Acrogonia nigriceps,* and on three species: *Graphocephala riverae* and *Gypona arunda*; and on two: *Agalliopsis imitans*, *Apogonalia fractinota*, *Stephanolla cazapana*, *Licontinia introducens* and *Empoasca alceda*. The subfamily of Cicadellidae with the largest number of species in our study was Cicadellinae with 11, which fed on 24 species of plants (53%) (Table I).

The plants species that supported the greatest number of leafhopper species and individuals were, *Anacardium excelsum* with six cicadellid species and 10 individuals, followed by *Castilla elastica* with three species and 14 individuals, and *Desmoncus orthacanthos* with two species and 11 individuals (Table I).

We compared the habitus of the plants on which the Cicadellidae fed. It was found that, according to estimates of Shannon Weiner, leafhopper communities on trees are more diverse than on shrubs or vines. The Simpson Index indicates that leafhopper communities are more diverse on trees and shrubs than on her habitus types (Table II). The Equitability Index indicates that the different communities are homogeneous in the distribution of the species Cicadellidae.

The PCA indicates that the trees (45.2%) and shrubs (29.2%) have a high percentage of variation (Figure 1) in the preference of food plants of leafhoppers.

Table II. Index of diversity for trees, shrubs, vines and grasses used by Cicadellidae.

Diversity Index	Trees	Shrubs	Vines	Grass	Fern
Taxa (S)	18	9	4	3	2
Individuals	69	20	21	4	4
Index Simpson (1-D)	0.8578	0.815	0.5669	0.625	0.375
Index Shannon (H)	2.299	1.917	1.077	1.04	0.5623
Equitability (J)	0.7954	0.8726	0.7767	0.9464	0.8113

DISCUSSION

The subfamily Cicadellinae presented the largest number of species in our study (11). They fed on 24 species of plants (Table I). According to Nielson & Knight (2000), Cicadellinae presents the greatest diversity of endemic genera in the Neotropical region, where many species feed on a wide range of plants, including herbs, trees, and shrubs, which has resulted in a large number of generalist species. Wolda (1979) fogged three *Luehea seemannii* trees and collected canopy insects, and found 10 subfamilies of Cicadellidae and 60 species, of which Cicadellinae presented 22 species. According to Wolda (1979) the fogging method is more effective in terms of number of individuals captured than the direct method (observation and sweep nets) that we used in this study; but in fogging we cannot know whether the insects were feeding on that tree, or on a liana, or was a casual visitor ("tourist").

All species of plants we observed were food plants, except *Castilla elastica*, which was host to all life stages of *Empoasca alceda*. A large population was found in the canopy, consisting of eggs, nymphs and adults on many leaves, specifically on the underside. *Empoasca* have a wide range of host plants, Poos & Wheeler (1943), reared 21 species of *Empoasca* on 108 species of host plants. *Empoasca* is a mesophyll feeding species, according to Claridge & Wilson (1978), and the nymphs of several leafhoppers that use this type of tissue can use a wide range of plants as food, as well as to reproduce on them.

Claridge et al. (1977) found that adult females of *Oncopsis* (Cicadellidae) discriminate between plants on which they fed and those on which they oviposit. They did experiments in which they placed females on non-host plants, where they died without laying eggs, indicating that oviposition behavior is related to a specific stimulus. Few studies have recorded the species of Cicadellidae and their hosts or food plants in non-agricultural areas. Paradell et al. (2012) collected at 112 sites and 21 provinces in Argentina (mostly agricultural areas), where 40 Proconiini species were found on 24 host families. Virla et al. (2008) found that *Oncometopia tucumana* is polyphagous, and has 12 species of host plants, belonging to 11 families.

The 67% from 24 species of this study were singletons. Similar results were found by Kishimoto-Yamada (2015) who studied the Hemiptera assembly in the canopy of a tropical forest in Borneo and found that 42% of adults were singletons. Basset et al. (2001) found in a study of abundance and diversity of herbivorous insects foraging on understory seedlings in a rainforest in Guyana, that most species were

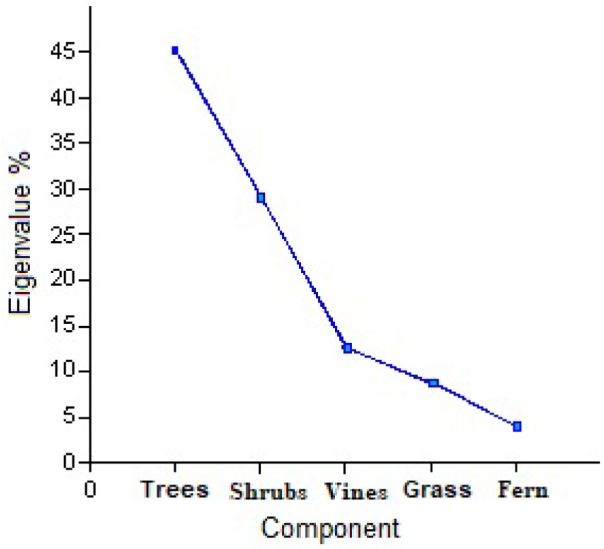

Figure 1. Principal component analysis showing the relationship between leafhoppers and plant habitus.

rare (38% singletons), with the lowest number of specimens for *Ladoffa ignota*. Novotný & Basset (2000) studied communities of tropical herbivorous insects and found 98 species (22%) of which were singletons. Although we sampled at different rainforest sites and along the vertical gradient, the percentage of singletons was high, perhaps due to poor sampling (Novotný & Basset 2000, Coddington et al. 2009, Kishimoto-Yamada et al. 2015).

Basset (1992) studied host specificity and found that there is a strong association between herbivorous insect communities and their rainforest hosts that may depend on: chemical traits of leaves (chemical defense and nutrient levels), availability of young leaves (factors related to plant phenology, abundance and growth strategy) and enemy-free space. Prestige & McNeill (1983) found that some of the Cicadellidae that feed on grasses are oligophagous and were associated with plant nitrogen levels, because they have different nitrogen requirements. In the case of Cicadellidae feeding on grasses, according to Prestige & McNeill (1983), most species occur on all species of grasses, but each grass has a particularly dominant fauna of Cicadellidae. Bennett & O'Grady (2012) found that 175 species of *Nesophrosyne* are highly host specific.

In our study *Ladoffa ignota* and *Soosiulus salutaris* were polyphagous, because they were fed on 13 and 15 plant species respectively. Adlerz (1980) found that *Homalodisca coagulata* (Cicadellidae) had 46 hosts. Lozada (1993) found in Peru two species of plants (*Axonopus scoparius* and *Pueraria phaseoloides*) that hosted 16 species of Cicadellidae belonging to five subfamilies; nine species were present on both species of plants.

In this study, the Shannon Wiener Index was highest in the tree communities (Table II). Ødegaard (2000) found a tendency for trees to support a larger number of wood-eating beetles than do lianas. Lowman et al. (1998) found that trees have more herbivores than the lianas in the canopy (7.4% vs 4.2%). According to PCA (Figure 1), the trees and shrubs showing a high variation in the food preference, because in some cases a same leafhoppers species were fed in two habitus (Table I), which indicates that there are many generalists.

The leafhoppers of the neotropical forest of Panama show preference feeding on food plants (mainly trees), they are polyphagous, their abundance is low and a high rate of singletons.

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E. Domínguez and V. Murillo contributed to the study design, have read and approved the manuscript. E. Domínguez, V. Murillo and J. Orwat conducted sampling. E. Domínguez analyzed the data and wrote the paper.

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