5 Folivorous Insects in the Rainforests of the Guianas

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Introduction

Unsurprisingly, insect–plant interactions in the neotropical region have been best studied where long-term taxonomic and ecological programmes exist at well-endowed research stations. In countries near the Guianas, this is evident in Costa Rica (e.g. Guanacaste Conservation Area: Janzen, 1983, 1988; La Selva: Marquis and Braker, 1993), Panama (e.g. Barro Colorado Island: Leigh, 1996), Puerto Rico (e.g. Luquillo Station: Reagan and Waide, 1996), Venezuela (Rancho Grande: Beebe and Crane, 1947; Huber, 1986), Trinidad (Simla Research Station, Arima Valley: Beebe, 1952) and Brazil (National Institute for Amazonian Research, INPA, at Manaus: Adis and Schubart, 1984; Adis, 1997). In contrast, long-term ecological programmes in French Guiana (e.g. Les Nouragues: Charles-Dominique, 1995; Poncy *et al.*, 1999), Suriname and Guyana (Mabura Hill: ter Steege *et al.*, 1996) rarely had the opportunity to generate substantial insect collections from rainforest habitats and concomitant studies on the ecology of insect herbivores. A notable exception may be the insect collections made at the Kartabo field station in Guyana which were, unfortunately, discontinued as early as 1924 (Beebe, 1925). As a consequence, the literature relating to insect–plant interactions in the rainforests of the Guianas is limited and, in addition, scattered in various sources dealing with insect, vertebrate or plant ecology and biology. Thus, the present compilation is unavoidably selective and represents only a starting point for more elaborate literature searches on specific insect–plant interactions.

Traditionally, insect–plant interactions are classified in the categories of either primary consumption ('herbivory') or mutualism, which largely overlap (e.g. Whitham *et al.*, 1991). Others have argued that moderate insect damage to plants can be beneficial in promoting growth and nutrient recycling (e.g. Owen, 1980). These views are rather phytocentric and may be of secondary interest to entomologists interested in elucidating patterns of host use by Guianan insects. The present review takes an entomocentric approach in order to stimulate deeper analyses of patterns of host use, as more and better data become available. The review concentrates on leaf and sap resources provided by vascular plants and used by folivorous insects (leaf-chewing and sap-sucking insects) in the rainforests of the Guianas (French Guiana, Suriname and Guyana). Other plant resources used by insects, such as epiphylls, flowers (see Chapter 6), seeds, extra-

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chap05.qxd 19/1/05 3:45 pm Page 296

floral nectaries, fruit bodies, stems (including ants nesting in stems, ant-gardens and phytotelmata), wood and roots, are not treated here. Papers focusing mainly on insect taxonomy or crop pests are not accounted for, unless reporting general patterns of host use or host records.

A brief outline of entomological activities in the rainforests of the three countries is essential to appreciate the degree to which our present knowledge of these insect–plant interactions may be biased towards particular insect groups and/or plant resources. Information available on the main groups of sap-sucking and leaf-chewing insects is then detailed. Particular sections are dedicated to leaf damage (herbivory) and to leaf-cutting ants, given the substantial information available on these popular subjects. We conclude in discussing several contentious issues particularly worthy of further investigation in the Guianas.

Rainforest Entomology in the Guianas: a Brief Outline

French Guiana

Entomological investigations in the rainforests of French Guiana have often been associated with the activity of isolated amateurs and professionals based in metropolitan France (e.g. Balachowsky, 1970). Many specimens from Maroni River and similar localities are also common in many major collections, including the Smithsonian and British museums. These mostly came via French dealers such as Le Moult (1955).

Recently, the laboratories of the Institut Français de Recherche Scientifique pour le Développement en Coopération (ORSTOM) at Cayenne and of the Institut National de Recherche Agronomique (INRA) at Kourou involved several entomological projects. Of relevance to this review, recent studies concentrated on the taxonomy of grasshoppers (Orthoptera) and on seedling attack by leaf-chewing insects. The 'Canopy Raft', a platform made of inflated beams and netting which allows access to the canopy, had two scientific missions in French Guiana, in 1989 and 1996 (see Hallé and Blanc, 1990; Hallé, 1998). Thus, there is some information on insect–plant interactions in the canopy (e.g. Delvare and Aberlenc, 1990; Lechat *et al.*, 1990; Sterck *et al.*, 1992; Dejean *et al.*, 1998; Lowman *et al.*, 1998). In addition, the grasshopper fauna of the forest canopy in French Guiana is well-known (see review in Amédégnato, 1997). In contrast, canopy collections and data are virtually non-existent for Suriname and Guyana, with the exception of samples obtained by the National Zoological Collection (see below) with yellow pan traps set up 10–25 m high in the canopy of Akintosoela, 80 km SSE of Paramaribo, as well as samples obtained from felled trees in a central rainforest of Guyana (Basset *et al.*, 1999).

The Department of Entomology of ORSTOM at Cayenne has one collection of Cerambycidae, including about 8000 specimens and 1500 species. The Laboratoire d'Environment Hydreco, created in 1990 with private funding from Electricité de France (EDF), owns a collection of about 1000 insect species and nearly 6000 specimens identified. However, many of the specimens collected in French Guiana are deposited in a few private collections and at the Museum National d'Histoire Naturelle, Paris, which is to establish an annexe near ORSTOM-Herbarium at Cayenne (see reviews in Amédégnato, 1997, 2003). Tavakilian (1993) reviews the state of knowledge of entomological research in French Guiana.

Suriname

The first scientific study of insect–plant interactions in the Americas may well be that of Maria Sybilla Merian (1705, 1719; Valiant, 1992), who was a remarkable naturalist and made beautiful illustrations of several Surinamese insects. She spent most of her time in coastal plantations and many of her rearings and illustrations concern crop insects, particularly moths and butterflies (Geijskes, 1951). Unfortunately, her nomenclature pre-dated that of Linnaeus,

chap05.qxd 19/1/05 3:45 pm Page 297

so that host records are difficult to extract from her studies.

More recently, entomological research in Suriname has been dominated by the studies of the resident Dutch entomologist Dirk Cornelis Geijskes, who was active from 1940 to 1986 (for a review of entomological activities in Suriname, see Geijskes, 1951, 1957). Although Geijskes was mainly interested in the taxonomy of dragonflies (Odonata), he made some general insect collections in rainforests (e.g. Geijskes, 1968) and studied some aspects of the biology of the leaf-cutting ants. Nowadays, a programme in bee ecology exists at the University of Suriname and studies of agricultural insect pests have been and are still prominent in the country.

The country has two sizeable insect collections. The National Zoological Collection of Suriname at the University includes a strong invertebrate section with about 1400 insect species, 900 of which are identified, and close to 10,000 individuals. Bee specimens are particularly well-represented. The collection is linked to a database which includes nearly 500 records on insect–plant interactions (Hiwat, personal communication). An additional 40,000 insect specimens collected from Atkintosula, 80 km SSE of Paramaribo (De Dijn, 2003), as well as a rainforest on laterite, have been sorted to various taxonomic levels and will be incorporated gradually in the general collections (De Dijn, 2003). In addition, information sources for entomologists at the library of the University are very good. The second collection is at the Agricultural Field Station of the Ministry of Agriculture and Fisheries, and holds approximately 4000 insect specimens. A few entomological monographs have been published in the journal *Studies on the Fauna of Suriname and other Guyanas*.

Guyana

The British Guiana Tropical Research Station at Kartabo was founded by the New York Zoological Society and was operated by William Beebe from 1916 to 1924 (Beebe, 1925). Extensive insect collections were made in the rainforest there (e.g. Beebe and Fleming, 1945; Fisher, 1944; Fleming, 1945, 1949, 1950). Miller (1994) considers Kartabo as one of the nine places in the neotropical region that had been sampled for moths fairly intensively during most months over a period of years. In addition, there have been several expeditions by entomologists based in the UK (e.g. O.W. Richards, Oxford University expedition, 1929), in the USA. (e.g. University of Michigan expedition; M. Collins, T.M. Forbes, P. Spangler, W. Steiner, F.X. Williams) or in Canada (H.S. Parish), so that the entomological fauna of Guyana is relatively well-known, although collections are scattered overseas. For example, a relatively comprehensive catalogue of butterflies was compiled for Guyana as early as 1940 (Hall, 1940).

Today, pest crops are the target of most entomological studies in Guyana and there is substantial information on leaf-cutting ants. Two sizeable insect collections exist in Guyana. The National Insect Collection is housed at the National Agricultural Research Institute, Mon Repos, East Coast Demerara. It includes 160 insect drawers, mostly including insect pests and associated enemies, but rainforest specimens are poorly represented (Munroe, 1993). The Center for Biodiversity at the University of Guyana houses a small collection of butterflies and about 21,000 specimens of rainforest insect herbivores collected at Mabura Hills, central Guyana. Entomological information relevant to Guyana can often be found in the journals *Timehri* and *Zoologica* (New York).

In short, the state of entomological knowledge in the Guianas cannot compare with that of other countries in Central and South America, particularly Costa Rica, Panama or Brazil. Overall, the insect fauna of Guyana is probably the best known of the three countries, but the best insect collections relevant to the Guianas may be found in Suriname, French Guiana, at the Museum d' Histoire Naturelle (Paris), the Natural History Museum (London), the

chap05.qxd 19/1/05 3:45 pm Page 298

Smithsonian Museum (Washington), the American Museum of Natural History (New York), the Zoological Museum (Leiden), the Museo del Instituto de Zoologia Agricola (Maracay) or the Museo E. Goeldi (Belem). Some taxonomic information exists for certain conspicuous, traditionally well-collected, insect taxa such as butterflies, moths and longicorn beetles. However, the paucity of taxonomic as well as ecological information on the main groups of rainforest folivores, Cicadellidae, Fulgoroidea, Chrysomelidae and some Curculionidae, is striking. Arguably, these groups, together with wood-boring insects (mainly Cerambycidae, Curculionidae and Scolytinae), represent an appreciable part of insect–plant interactions and biodiversity in the rainforests of the Guianas.

Sap-sucking Insects

Thysanoptera and Heteroptera

Rainforest host-plant records in the literature for sap-sucking insects in the Guianas are probably very incomplete and all originate from Guyana (Table 5.1). Although sap-sucking insects (Thysanoptera and Hemiptera) are the main sap consumers in rainforests, leaf-cutting ants (see later) often ingest directly the sap from cut leaves (Littledyke and Cherrett, 1976) and studies by Cherrett (1980) showed that this represents an appreciable part of energy requirements of a colony. Information about Thysanoptera is limited to a general account originating from Suriname, without host-plant records (Priesner, 1923). In the rainforests near Kartabo, Beebe (1925) considered the Pentatomidae, Coreidae and Lygaeidae dominant among herbivorous heteropterans. In Suriname, van Doesburg (1966) treated the families Largidae and Pyrrhocoridae, detailed some host records and, in particular, indicated that some species of largids feed on *Inga* spp. (Mimosaceae).

Auchenorrhyncha and Stenorrhyncha

In Kartabo, the most abundant homopterans include Cicadellidae, Membracidae, Coccoidea and Cercopidae (Beebe, 1925), while Cicadellidae, Membracidae, Achilidae and Ciixidae are particularly abundant in the understorey near Mabura Hills (Charles, 1998; Basset and Charles, 2000). Limited information is available on the mealybugs collected near Kartabo, particularly the species feeding on ant plants (Morrison, 1922). Some species appear to be wide generalists (Table 5.1). Another source of information for the mealybugs of the Guianas is Williams and Willink (1992), although this targets mostly pests of various crops and economic plants (but see one record in Table 5.1).

Metcalf (1945) reported about 39 species of Fulgoroidea collected in the rainforests near Kartabo. Many species are also found elsewhere in Central and South America, but no host records are available. Similarly, Metcalf (1949) reported on 23 species of xylem-feeding Cicadellidae (Tettigellidae and Gyponidae, now in subfamily Cicadellinae) collected at Kartabo, without mention of host records. Haviland (1925) collected 75 species of Membracidae collected at Kartabo during a 5-month period. The salient features of this fauna include the wide geographical distribution of the species, preference of most species for clearings over deep shade forest, many species being attended by ants but when unattended, being solitary as adults. Haviland provided only two host records (Table 5.1), but suggested that many species were monophagous, or at least restricted to a few species of plants. However, published host records of sap-sucking insects in Mabura Hill, Guyana, indicated a larger range of plants used, particularly for Cicadellidae, Membracidae and Cixiidae (Basset and Charles, 2000; Table 5.1). The studies of Haviland (1925) and Funkhouser (1942) stress that many Membracidae found in Guyana are widely distributed in South America.

Table 5.1. Host-plant records indicated in the literature for sap-sucking insects in the Guianas. All records originate from Guyana. See additional information in the text.

Insect species	Family	Host-plant(s)[a]	Source
Herpis vittata F.	Derbidae	A, B, C, D, E	Basset and Charles, 2000
Plectoderes collaris F.	Achilidae	A, B, C, D, E	Basset and Charles, 2000
Sevia bicarinata F.	Achilidae	A, B, C, D, E	Basset and Charles, 2000
Sevia consimile Fennah	Achilidae	A, B, C, D, E	Basset and Charles, 2000
Taosa muliebris Walker	Dictyopharidae	B, E	Basset and Charles, 2000
Toropa ferrifera (Walker)	Dictyopharidae	A, B, C, D, E	Basset and Charles, 2000
Toropa picta Walker	Dictyopharidae	B, E	Basset and Charles, 2000
Nogodina reticulata F.	Nogodinidae	A, B, C, D, E	Basset and Charles, 2000
Boethoos globosa Haviland	Membracidae	*Vismia ferruginea* Kunth (Clusiaceae)	Haviland, 1925
Darnis lateralis F.	Membracidae	A, B, C, D, E	Basset and Charles, 2000
Endoastus productus Osborn	Membracidae	*Tachigali paniculata* Aubl. (Caesalpiniaceae)	Osborn, 1921
Potnia gladiator Walker	Membracidae	A, C, E	Basset and Charles, 2000
Stegaspis fronditia L.	Membracidae	B, E	Basset and Charles, 2000
Tragopa guianae Haviland	Membracidae	*Vismia ferruginea* Kunth	Haviland, 1925
Acrocampsa pallipes F.	Cicadellidae	A, B, C, D, E	Basset and Charles, 2000
Amblyscarta invenusta Young	Cicadellidae	A, B, C, D, E	Basset and Charles, 2000
Baluba parallela Nielson	Cicadellidae	A, B, C, D, E	Basset and Charles, 2000
Barbatana extera Freytag	Cicadellidae	A, B, D	Basset and Charles, 2000
Cardioscarta quadrifasciata L.	Cicadellidae	A, B, C, E	Basset and Charles, 2000
Dasmeusa basseti Cavichioli and Chiamolera	Cicadellidae	A, B, C, D, E	Basset and Charles, 2000
Dasmeusa pauperata Young	Cicadellidae	A, B, C, D, E	Basset and Charles, 2000
Docalidia o'reilly Nielson	Cicadellidae	D, E	Basset and Charles, 2000
Gypona bulbosa DeLong and Freytag	Cicadellidae	A, B, C, D, E	Basset and Charles, 2000
Gypona flavolimbata Metcalf	Cicadellidae	A, C, D	Basset and Charles, 2000
Gypona flavolimbata Metcalf	Cicadellidae	A, C, E	Basset and Charles, 2000
Gypona funda DeLong	Cicadellidae	B, C	Basset and Charles, 2000
Gypona glauca F.	Cicadellidae	B, C, E	Basset and Charles, 2000
Gypona offa DeLong and Freytag	Cicadellidae	C	Basset and Charles, 2000
Joruma coccinea McAtee	Cicadellidae	A, B, C, E	Basset and Charles, 2000
Ladoffa aguilari Lozada	Cicadellidae	A, B, C, D, E	Basset and Charles, 2000
Ladoffa comitis Young	Cicadellidae	A, B, C, D, E	Basset and Charles, 2000
Ladoffa ignota Walker	Cicadellidae	A, B, C, D, E	Basset and Charles, 2000

Table 5.1. *continued*

Insect species	Family	Host-plant(s)[a]	Source
Macugonalia moesta (F.)	Cicadellidae	A, B, C, D, E	Basset and Charles, 2000
Mattogrossus colonoides (Linnavuori)	Cicadellidae	A	Basset and Charles, 2000
Planocephalus flavicosta (Stal.)	Cicadellidae	A, E	Basset and Charles, 2000
Poeciloscarta cardinalis F.	Cicadellidae	A, B, C, D, E	Basset and Charles, 2000
Soosiulus fabricii Metcalf	Cicadellidae	A, B, C, D, E	Basset and Charles, 2000
Soosiulus interpolis Young	Cicadellidae	A, B, C, D, E	Basset and Charles, 2000
Xedreota tuberculata (Osborn)	Cicadellidae	A, B, C, D, E	Basset and Charles, 2000
Xestocephalus desertorum (Berg)	Cicadellidae	A, E	Basset and Charles, 2000
Cryptostigma quinquepori (Newstead)	Coccidae	*Cecropia*, *Ficus*, *Pithecellobium*, *Microlobium*	Newstead, 1917a; Morrison, 1922
Akermes secretus Morrison	Coccidae	*Inga*, *Haematoxylum*, *Triplaris*	Morrison, 1922
Ceroplastes cirripediformis Comstock	Coccidae	*Argyreia nervosa*, *Hura crepitans* (generalist)	Newstead, 1917b
Eucalymnatus decemplex (Newstead)	Coccidae	*Lecythis* sp. (Lecythidaceae)	Newstead, 1920
Saissetia hurae (Newstead)	Coccidae	*Hura crepitans* L. (Euphorbiaceae)	Newstead, 1917a
Lecanodiaspis ingae Howell and Kosztarab	Lecanodiaspididae	*Inga* spp. (Mimosaceae)	Howell and Kosztarab, 1972
Cataenococcus rotundus (Morrison)	Pseudococcidae	*Cecropia angulata* I.W. Bailey (Cecropiaceae)	Williams and Willink, 1992
Dysmicoccus probrevipes (Morrison)	Pseudococcidae	*Cordia*, *Tachigali*	Morrison, 1929
Farinococcus multispinosus Morrison	Pseudococcidae	*Triplaris*, *Cecropia*	Morrison, 1922
Pseudococcus bromeliae Bouché	Pseudococcidae	*Tachigali*, *Cecropia*, *Cordia*, *Ananas*	Wheeler, 1921; Morrison, 1922
Trionymus petiolicola (Morrison)	Pseudococcidae	*Tachigali paniculata* Aubl.	Morrison, 1922
Arocera equinoxia (Westwood)	Pentatomidae	B, C, D, E	Basset and Charles, 2000
Mormidea ypsilon (L.)	Pentatomidae	E	Basset and Charles, 2000

[a]A=*Chlorocardium rodiei* (Scomb.), B=*Mora gonggrijpii* (Kleinh.) Sandw., C=*Eperua rubiginosa* Miq., D=*Pentaclethra macroloba* (Willd.) O. Kuntze, E=*Catostemma fragrans* Benth.

chap05.qxd 19/1/05 3:45 pm Page 301

Recently, the sap-sucking insects feeding on the seedlings of five common tree species have been studied near Mabura Hill, Guyana, on a relatively large scale: *Catostemma fragrans* Benth. (Bombacaceae), *Chlorocardium rodiei* (Scomb.) (Lauraceae), *Eperua rubiginosa* Miq., *Mora gonggrijpii* (Kleinh.) Sandw. (both Caesalpiniaceae) and *Pentaclethra macroloba* (Willd.) O. Kuntze (Mimosaceae) (Basset 1999, 2000; Basset and Charles, 2000). Monthly surveys of almost 10,000 seedlings were performed over a 2-year period in a forest plot of 1 km^2. Collections included over 24,000 specimens and 425 species. The most speciose families were Cicadellidae (including many Cicadellinae, Coelidiinae and Idiocerinae), Derbidae, Membracidae (particularly Smiliinae), Achilidae and Cixiidae. The most abundant families were Psyllidae, Cicadellidae, Cixiidae, Derbidae and Pseudococcidae. Plataspididae were the only conspicuous family of Heteroptera, being abundant but not speciose. A small fraction of the material was identified to species level (Table 5.1). Although feeding records are difficult to ascertain in most cases, the magnitude of collections allow inference of some degree of host specificity. Some species are almost certain to be wide generalists. For example, among Cicadellidae, a striking pattern was the high proportion of Cicadellinae in the collections, which are all xylem-feeders and often highly polyphagous (Basset, 1999, 2000; Basset and Charles, 2000; Basset *et al.*, 1999, 2001). Many such species were collected from the five hosts studied and observed feeding *in situ*. On *E. rubiginosa*, the dominant sap-sucking insect was a unidentified species of *Isogonoceraia* (Psyllidae) (Hollis, personal communication). Similarly, Gombauld (1996) observed that in French Guiana, among sap-sucking insects feeding on the seedlings of *Eperua grandiflora* (Aubl.), Psylloidea were the dominant group.

Herbivory

In the understorey, Newbery and de Foresta (1985) observed that the percentage of leaf area lost to herbivores was greater in the primary forest than in pioneer vegetation at La Piste de St Elie in French Guiana. In total, it averaged 5.5% of leaf area lost. Mature leaves of the shaded forest understorey were more heavily grazed than those on pioneer trees and those on small trees which grew in large, well-illuminated gaps. In the canopy, Sterck *et al.* (1992) measured herbivory among trees, lianas and epiphytes at the stations of Petit Saut and Les Nouragues in French Guiana. Overall damage levels of both canopies were just over 5%, individual samples ranging from 0.8% to 12.8% damage, without clear differences between life forms. Similarly, Lechat *et al.* (1990) measured leaf damage in a transect from the ground to the canopy at Petit Saut. Individual samples ranged from 0% to 20%, but 90% of the samples had below 10% damage and 60% below the 5% damage level. Leaf damage was not correlated with the height of the samples. On average, preliminary results of Lowman *et al.* (1998) indicated 4.7% damage in the canopy near Paracou, with trees supporting vines averaging over twice as much herbivory than trees devoid of vines.

Gombauld and Rankin de Merona (1998) measured leaf damage on *Eperua falcata* (Aubl.), *E. grandiflora, Dicorynia guianensis* Amshoff (Caesalpiniaceae), *Goupia glabra* Aubl. (Celestraceae) and *Qualea rosea* Aubl. (Vochysiaceae) by tagging leaves at Paracou (and see Gombauld, 1996). For *E. falcata*, in non-limiting light conditions (as in tree fall gaps), low levels of insect damage on leaves is correlated with increased height and stem diameter growth, whereas high levels of damage are correlated with a decrease in these parameters. *E. grandiflora*, which depends on cotyledon reserves for growth, is not influenced by damage by leaf-eating insects (Gombauld, 1996). Among the five species studied, *D. guianensis* is unique in main-

chap05.qxd 19/1/05 3:45 pm Page 302

taining leaf production throughout the dry season. In this case, the relative impact of herbivory is reduced during the period when ground water deficits create conditions unfavourable for plant growth. *E. falcata*, *E. grandiflora* and *Q. rosea* experience high levels of herbivory during the dry season and display significantly lower mean height growth during the rainy season than during the dry season. In contrast, *D. guianensis* and *G. glabra* have similar height growth regardless of the season. Despite the rainy season being the more favourable period for the activity of leaf-eating insects (Gombauld, 1996), ratios of damage (leaf area eaten/total leaf area) do not differ significantly between the rainy and the dry season, with the exception of *E. grandiflora*. This pattern confirms that the proportion of leaf area produced and eaten varies similarly during the year (Gombauld and Rankin de Merona, 1998).

In Guyana, Isaacs *et al.* (1996) measured apparent leaf damage on *Dicymbe altsonii* Sandw. (Caesalpiniaceae), which forms monodominant stands on bleached sand soils (albic arenosols). Across four transects, damage ranged from 10.7% to 12.9% and leaf-cutting ants accounted for about half of the leaf area lost. Ter Steege (1990) mentioned that leaf damage was <10% for most seedlings of another Caesalpiniaceae, Morabukea (*Mora gonggrijpii*) at Mabura Hill, Guyana, though the level of apparent damage, due mainly to leaf-scraping Chrysomelidae and leaf-chewing Tettigoniidae, increases considerably in large treefall gaps (Hammond, unpublished data), possibly due to an increase in young leaf availability. On Maracá Island, in Roraima, Brazil (bordering Guyana), Nascimento and Proctor (1994) measured herbivory on *Peltogyne gracilipes* Ducke (Caesalpiniaceae). *P. gracilipes* forms monodominant stands on this river island and related species of *Peltogyne* are common in the Guianas (Hammond *et al.*, 1996). Apparent leaf damage on *P. gracilipes* amounted to 11.4%, but in 1992 severe defoliation occurred. Nearly 60% of trees showed heavy and extreme damage (from 50% and greater of the crown defoliated). The insect responsible was *Eulepidotis phrygionia* Hampson, a generalist moth (Noctuidae), which is widespread in Brazil.

Coley and Aide (1991) reviewed herbivory in temperate and tropical forests and found that annual rates of herbivory in the latter amounted to 10.9%. Therefore, available data for the Guianas suggest that levels of herbivory there may not be extremely different from those elsewhere in the tropics, with perhaps a tendency to be lower. Both Newbery and de Foresta (1985) and Sterck *et al.* (1992) remarked that, being measured in the dry season, level of leaf damage may have been underestimated. Indeed, leaf damage in French Guiana is often higher in the late wet and early dry seasons when new leaves are produced than during the dry season (Gombauld, 1996; on Panama, see also Aide, 1988). This also correlates with the seasonality of large leaf-chewing insects, such as grasshoppers, whose densities are highest during that period of the year (Amédégnato, personal communication). A second complication is that all the values reported for the Guianas, with the exception of Gombauld (1996), concern apparent leaf damage (percentage of area lost), which typically does not account for leaves eaten entirely and therefore underestimates leaf damage (e.g. Lowman, 1984). This could be a serious bias when densities of large-bodied leaf-chewing insects, such as grasshoppers, are locally high. In these instances, whole herbaceous plants can be consumed within 2 h (Amédégnato, personal communication). Monitoring grazing rates by tagging leaves is an alternative to this problem (Lowman, 1984).

Leaf-chewing insects

Leaf-chewing insects include mostly grasshoppers, stick insects, beetles, moths, butterflies, sawflies and leaf-cutting ants (see below). Host records for these rainforest insects in the Guianas are summarized in Table 5.2.

Table 5.2. Host-plant records indicated in the literature for leaf-chewing insects in the Guianas. See additional information in the text.

Insect species	Family	Host-plant(s)	Country	Source
Colpolopha spp.	Romaleidae	Dicotyledones (generalist)	French Guiana	Descamps, 1978, 1979[a]
Maculiparia guyanensis Amedegnato	Romaleidae	Monocotyledones (specialist)	French Guiana	Descamps, 1978, 1979[a]
Phaeoparia lineaalba L	Romaleidae	Monocotyledones (specialist)	French Guiana	Descamps, 1978, 1979[a]
Abacris flavalineata (De Geer)	Acrididae	*Eperua grandiflora* (Aubl.) (Caesalpiniaceae)	French Guiana	Gombauld, 1996
Clematodina sastrei Amedegnato & Descamps	Acrididae	Dicotyledones (generalist)	French Guiana	Descamps, 1978, 1979[a]
Copiocera spp.	Acrididae	*Euterpe oleracea* Mart. (Arecaceae)	French Guiana	Amédégnato, 1996
Cryptocloeus fuscipennis Bruner	Acrididae	*Loreya mespiloides* Miq. (Melastomataceae)	French Guiana	Descamps, 1978, 1979[a]
Ommatolampis perspiscillata Johanssen	Acrididae	Dicotyledones (generalist)	French Guiana	Descamps, 1978, 1979[a]
Prionolopha serrata (L.)	Acrididae	*Eperua falcata* (Aubl.), *E. grandiflora*	French Guiana	Gombauld, 1996
Schistocerca pallens (Thunberg)	Acrididae	*Eperua falcata*	French Guiana	Gombauld, 1996
Arawakella unca Rehn and Rehn	Eumastacidae	*Vismia* sp. (Clusiaceae)	French Guiana	Descamps, 1978, 1979[a]
Eneoptera guyanensis Chopard	Gryllidae	*Eperua grandiflora*	French Guiana	Gombauld, 1996
Lutosa brasiliensis (Brunner)	Tettigoniidae	*Eperua falcata* (Aubl.) (Caesalpiniaceae)	French Guiana	Gombauld, 1996
Huradiplosis surinamensis Nijveldt	Cecidomyiidae	*Hura crepitans* L. (Euphorbiaceae)	Suriname	Nijveldt, 1968
Asphaera abbreviate F.	Chrysomelidae	*Dicorynia guianensis*, *Eperua falcata*	French Guiana	Gombauld, 1996
Asphaera nobilitata F.	Chrysomelidae	*Eperua falcata*, *E. grandiflora*	French Guiana	Gombauld, 1996
Chalcophyma collaris Lef.	Chrysomelidae	*Eperua falcata*, *E. grandiflora*	French Guiana	Gombauld, 1996
Chalcophyma fulgida Lef.	Chrysomelidae	*Eperua falcata*	French Guiana	Gombauld, 1996
Chalcophyma tarsalis Baly	Chrysomelidae	*Eperua falcata*	French Guiana	Gombauld, 1996
Coelomera cajennensis F.	Chrysomelidae	*Cecropia peltata* L. (Cecropiaceae)	Guyana	Bodkin, 1919
Cryptocephalus esuriens Suffrian	Chrysomelidae	*Mora*, *Eperua*, *Pentaclethra*, *Catostemma*	Guyana	Basset and Charles, 2000
Naupactus albulus Boheman	Curculionidae	*Eperua falcata*	French Guiana	Gombauld, 1996
Naupactus bellus Hustache	Curculionidae	*Dicorynia*, *Eperua*, *Goupia*, *Qualea*	French Guiana	Gombauld, 1996
Naupactus ornatus Schönherr	Curculionidae	*Eperua falcata*	French Guiana	Gombauld, 1996
Plectrophoroides unicolor Chevrolat	Curculionidae	*Eperua falcata*	French Guiana	Gombauld, 1996
Eurytides ariarathes Esper	Papilionidae	*Rollinia* sp. (Annonaceae)	French Guiana	Brévignon, 1990
Eurytides protesilaus (L.)	Papilionidae	*Duroia eriopila L.* (Rubiaceae)	Suriname	Merian, 1705
Papilio torquatus Cramer	Papilionidae	*Moniera trifolia* L. (Rutaceae)	French Guiana	Brévignon, 1990
Phoebis sennae (L.)	Pieridae	*Inga ingoides* (L.C. Richard) Will. (Mimosaceae)	Suriname	Merian, 1705
Lycorea ilione Cramer	Nymphalidae	*Ficus* spp. (Moraceae)	Guyana	Ackery, 1988
Napeocles jucunda Hübner	Nymphalidae	*Ruellia inflata* Rich. (Acanthaceae)	French Guiana	Brévignon, 1990
Chalybs janais (Cramer)	Lycaenidae	*Pentaclethra macroloba* (Mimosaceae)	Guyana	Basset and Charles, 2000
Thestius phloeus (Cramer)	Lycaenidae	*Vouacapoua americana*, *Catostemma fragrans*	F. Guiana, Guyana	Joly, 1996; Basset and Charles, 2000

Table 5.2. *continued*

Insect species	Family	Host-plant(s)	Country	Source
Cremna thasus Stoll	Riodinidae	*Tilliandsia bulbosa* Hook (Bromeliaceae)	French Guiana	Brévignon, 1992
Euselasia thusnelda Möschler	Riodinidae	*Caraipa* (Clusiaceae)	French Guiana	Brévignon, 1995, 1997
Euselasia arcana Brévignon	Riodinidae	*Clusia* (Clusiaceae)	French Guiana	Brévignon, 1995, 1997
Euselasia euryone (Hewitson)	Riodinidae	*Mahurea* (Clusiaceae)	French Guiana	Brévignon, 1995, 1997
Euselasia midas F.	Riodinidae	*Tovomita* (Clusiaceae)	French Guiana	Brévignon, 1995, 1997
Napaea beltiana Bates	Riodinidae	*Catasetum barbatum* Lindl. (Orchidaceae)	French Guiana	Brévignon, 1992
Arsenura armida (Cramer)	Saturniidae	*Erythrina fusca* Loureio (Fabaceae)	Suriname	Merian, 1705
Syssphinx molina Cramer	Saturniidae	*Inga* sp. (Mimosaceae)	Suriname	Robinson and Kitching, 1997
Aleuron carinata Walker	Sphingidae	*Ambelania tenuiflora* Muell. Arg. (Apocynaceae)	French Guiana	Robinson and Kitching, 1997
Oryba kadeni Schaufuss	Sphingidae	*Palicourea* sp. (Rubiaceae)	French Guiana	Robinson and Kitching, 1997
Thysania agrippina (Cramer)	Noctuidae	*Bursea simaruba* (L.) (Burseraceae)	Suriname	Merian, 1705
Atomacera pubicornis F.	Argidae	*Ipomoea* sp. (Convolvulaceae)	Guyana, Suriname	McCallan, 1953; Smith, 1992
Hemidianeura leucopoda Cameron	Argidae	*Inga* sp. (Mimosaceae)	Guianas	Smith, 1992
Ptilia brasiliensis Lepeletier	Argidae	*Lecythis* sp. (Lecythidaceae)	French Guiana	McCallan, 1953; Smith, 1992
Ptilia peletieri Gray	Argidae	*Cnestidium rufescens* Planch. (Connaraceae)	Guyana, Suriname	Benson, 1930; Smith, 1992
Themos surinamensis Klug	Argidae	*Ceiba pentandra* (L.) Gaertn. (Bombacaceae)	Guianas	Smith, 1992

[a]And C. Amedegnato, Paris, 1998, personal communication.

chap05.qxd 19/1/05 3:45 pm Page 305

Phasmids and Orthoptera

Host records for rainforest Phasmida in the Guianas proved difficult to find. In French Guiana, the communities of arboricolous grasshoppers (Orthoptera: Acridoidea) do not appear to be very different from elsewhere in Amazonia (Amédégnato and Descamps, 1980). Typically, these communities include a high number of very closely related sympatric species which often live on the same tree (Amédégnato, 1997). Descamps (1978) recorded at least 44 genera and 57 species in the families Romaleidae, Acrididae, Eumastacidae and Proscopiidae (in order of decreasing importance) from these communities. Grasshopper density in tree crowns appears relatively low: on average, 22 individuals and 10 species per tree (i.e. about 0.2–0.5 individual per m^2 of leaf area) in the Amazon, reaching 16.5 individuals per tree in French Guiana in particular. Grasshopper species richness is lowest on nutrient-poor soils in French Guiana (Amédégnato, personal communication). Densities also appear to be higher in the upper canopy than in the mid canopy or understorey (Amédégnato, 1997, 2003). Most grasshoppers either feed on tree foliage, or bark and small epiphytes, or on larger epiphytes.

However, host-plant records are rare (Table 5.2). Many species are rather polyphagous, such as most Eumastacidae. Of particular interest is the specialization on palms of a number of species within the Copiocerae (Acrididae). In the Guianas, this concerns about 10 species in the genera *Copiocerina*, *Copiocera* and *Eumecacris* (Amédégnato, 1996). Usually, Lauraceae, Combretaceae and Myristicaceae support a rich and abundant grasshopper fauna, in contrast with Leguminosae and Lecythidaceae (Amédégnato, 1997).

Coleoptera and Diptera

Beebe (1925) commented on the richness of the phytophagous beetle families Chrysomelidae and Curculionidae in Kartabo, stating that the variety of the former was 'unbelievable'. Chrysomelidae were the most species-rich and abundant leaf-chewing taxa feeding on seedlings in Central Guiana (Basset and Charles, 2000). Unfortunately, the present state of taxonomic knowledge of the rainforest material in the Guianas, particularly Chrysomelidae, precludes any useful analysis beyond Beebe's enthusiastic statement (Jolivet, personal communication). However, one particular genus of Galerucinae has been relatively well-studied. At least 35 species of *Coelomera* (Chrysomelidae, Galerucinae) are known to feed on *Cecropia* spp. and other Cecropiaceae, and are widely distributed in the neotropical region (Jolivet, 1987). Unfortunately, the confusing state of the taxonomy of both *Coelomera* and *Cecropia* does not allow to investigate whether there is a one-to-one correspondence between the beetle and the plant species (Jolivet, 1987). Jolivet and Salinas (1993) described oviposition by *C. cajennensis* F. inside the internodes of *C. peltata* L. in Venezuela, in a fashion similar to that of the ants inhabiting the hollow twigs. The outcome of this behaviour appears to be an improved protection of the egg masses. The larvae are free-living and often considerably damage the leaves of their host plant. Adults avoid ants by reflex bleeding, or thanatosis, and their larvae by enteric or buccal discharge. In particular, the larvae of some species exhibit a peculiar form of defence, cycloalexy (Vasconcellos-Neto and Jolivet, 1994). They form a circle, head to head, and their supra-anal shields and enteric secretions at the periphery of the circle protect them against ant or bug attack. Depending on local conditions, ants and beetles may cohabit or exclude themselves on the foliage, but this situation is not well understood (Jolivet, 1987, 1989).

Records of rainforest Curculionidae and Diptera feeding on leaves in the Guianas were even more difficult to extract from the literature (Table 5.2). In particular, literature on insect galling and leaf-mining in the Guianas is very limited, other than Nijveldt's (1968) description of one gall midge from Suriname (Table 5.2).

chap05.qxd 19/1/05 3:45 pm Page 306

Lepidoptera

Although there is considerable taxonomic information about the moth fauna of the Guianas, the larval biology of most species is unknown. For example, in French Guiana, Haxaire and Rasplus (1986, 1987) list 50 species of Sphingidae and de Toulgoet (1987) lists 200 species of Arctiidae, but no host-plant information is provided. De Jong (1983) lists 426 reported species of Hesperiidae in Suriname and stresses the wide distribution of most species in South America. Similarly, Lindsey (1928), Beebe and Fleming (1945) and Fleming (1945, 1949, 1950) provide species lists for several moth and butterfly families at Kartabo. Beebe (1925) further reported that Noctuidae, Geometridae and Pyralidae collected at lights at Kartabo represent about 55% of the species richness in macrolepidopteran moths, so it is probable that these families also contribute in large part to the caterpillar fauna in rainforests, although care must be taken extrapolating from such data. Further, Beebe (1925) considers Ithomiinae and Heliconinae (both in Nymphalidae) to be typical butterfly taxa belonging to the rainforest habitat, and Pieridae and Hesperiidae to be also common butterfly families in the rainforests near Kartabo.

The few host records available in the butterfly catalogue for Guyana (Hall, 1940) include records from crops and orchard trees. The information more particularly relevant to rainforest butterflies often needs to be tracked in the databases and rearing reports of keen professional and amateur lepidopterists (Table 5.2). Of interest, the few host records available involving epiphytic plants mainly concern riodinid butterflies (e.g. Brévignon, 1992; Table 5.2).

Hymenoptera

Knowledge of the phytophagous sawflies (Hymenoptera, 'Symphyta') of the Guianas is extremely limited. At least 60 species have been recorded from the Guianas in the families Argidae, Pergidae and Tenthredinidae, although the exact number is likely to be many times greater (Benson, 1930; McCallan, 1953; Smith, 1988, 1990, 1992). The faunas are best known from Guyana, but very little is known about their ecology, particularly the host plants of the larvae (Table 5.2). Of the recorded species, the majority are found within the genera *Scobina*, *Hemidianeura*, *Manaos*, *Ptilia* (all Argidae), *Perreyiella*, *Decameria*, *Aulacomerus* (all Pergidae), *Stromboceros*, *Adiaclema* and *Waldheimia* (all Tenthredinidae).

It is probable that phytophagous species of the parasitoid superfamilies Cynipoidea and Chalcidoidea are more common in the Guianas than the data in the collections and the literature suggest. For example, the genus *Eschatocerus*, of the gall-forming Cynipidae (Cynipoidea), is rather diverse and, usually, host-specific on certain Leguminosae (Fergusson, personal communication). Leaf-cutting ants of the tribe Attini (Formicidae) are discussed later.

Studies of Particular Host Plants

Leaf-chewing insects feeding on the seedlings of several tree species have been relatively well-studied in French Guiana. Mature leaves of *Eperua* spp. are not greatly damaged by insects, and herbivory does not appear to cause major seedling mortality in comparison with the effect of vertebrate herbivores. In contrast with young leaves of *E. falcata*, those of *Eperua grandiflora* are damaged frequently by invertebrate herbivores, and are often defoliated totally, leading to high seedling mortality (Forget, 1992). Gombauld (1996) studied in more detail the insect herbivores feeding on the seedlings of *E. falcata* and *E. grandiflora* at Paracou, French Guiana. Patterns of attack and consequences for seedling growth and survival were contrasted between different treatments and canopy openness. A total of 16 leaf-chewing species were collected from the families Tettigoniidae (genus *Lutosa*), Acridoidea (*Abacris*, *Prionolopha*, *Schistocerca*, *Colpolopha*), Gryllidae (*Eneoptera*), Chrysomelidae (Eumolpinae:

chap05.qxd 19/1/05 3:45 pm Page 307

Chalcophyma; Alticinae: *Asphaera*), Curculionidae (Entiminae: *Naupactus*, *Plectrophoroides*) and Saturniidae. Few species appeared to be host specific and Gombauld noted that *Asphaera* and *Naupactus*, for example, are feeding on other tree species (*Goupia*, *Dicorynia*, *Qualea*). Leaf damage appeared occasional, without permanent setting on the seedlings. Chrysomelids were the dominant group of leaf-chewing insects on *Eperua*, but it was not known whether herbivores were restricted to the understorey or fed also on *Eperua* leaves in the canopy. Rates of attack on *Eperua* seedlings were correlated positively with leaflet production and sometimes increased at higher seedling densities. However, damage remained low in the primary forest, presumably since secondary hosts for eumolpine beetles were less common there. Gombauld also stressed that *Eperua* seedlings represent a low resource for herbivorous insects and that the energy needed for insect dispersal and feeding may be considerable. This pattern was similar for insects feeding on seedlings in Mabura Hill (Basset, 1999, 2000). The case of *E. grandiflora* is interesting; since its seeds are dispersed by various rodents (Forget, 1992), seedlings may sometimes establish at some distance from the parent trees. In this situation, Gombauld (1996) predicted that populations of specialist insects would become more fragmented (and less successful) with increasing distance between individuals.

Forget (1994, 1996) studied the seedling dynamics of *Vouacapoua americana* (Caesalpiniaceae) at Piste de St Elie, and assumed that a majority of seedlings died due to development of fungi on stems observed during the establishment phase. Complementary observations were made by Joly (1996) in Les Nouragues, where young red leaves of sprouting seedlings of *V. americana* were heavily attacked (up to 100%) by *Thestius pholeus* (Cramer) (Lycaenidae) in June–July, i.e. in the late wet season. This species appears to be rather host-specific and it did not consume either mature leaves or other leaves sampled at random in the understorey (Joly, 1996; but consider an observation made in Guyana below). In addition, the intensity of attack by the caterpillar was not evenly distributed, and only *V. americana* seedlings growing in areas with high density of conspecific trees were damaged (Joly, personal communication). It is possible that the occurrence of the caterpillar is related to the density of *V. americana* and/or overall tree diversity at the community level, both of which may vary widely between forest areas, thus having different impact between sites. Given that *V. americana* may form dense patches, as well as other similarly large-seeded species in the Guianas (e.g. *Chlorocardium rodiei*) that are subjected to insect herbivory, it would be interesting to quantify the impact of such herbivores on juvenile recruitment in light of tree patch density.

Although many species of *Cecropia* are inhabited by ants, this genus has been deemed 'the most hospitable tree of the tropics' (Skutch, 1945). Many animal species feed on its leaves, nectar and inflorescences, food bodies and on the ants themselves. The insect fauna feeding on *Cecropia* spp. is reasonably well-known (e.g. Fiebrig, 1909; Wheeler, 1942; Jolivet, 1987) and includes many species of Aleyrodidae, Chrysomelidae, Curculionidae and Nymphalidae, but few records originate from the Guianas.

The leaf-chewing insects feeding on the seedlings of various tree species were studied rather extensively at Mabura Hill, Guyana (Basset, 1999; Basset and Charles, 2000). Collections included over 3100 specimens, 179 species and 16 insect families. The most abundant and speciose families included Chrysomelidae (particularly Galerucinae, Eumolpinae, Alticinae and Cryptocephalinae) and Curculionidae (particularly Entiminae). The majority of the remainder included 13 families of Lepidoptera, with Gelechiidae dominating. Many of these species, particularly among Eumolpinae and Entiminae, were able to feed on the seedlings of the five hosts studied. Interestingly, the lycaenid *Thestius pholeus*, which severely damage the seedlings of *V. americana* in French Guiana

chap05.qxd 19/1/05 3:45 pm Page 308

(Joly, 1996), also attacks the young foliage of seedlings of *C. fragrans* at Mabura Hill (but more commonly saplings of the same species), and that of an unknown vine (Basset, personal observation). With the exception of Orthoptera (the collections targeted diurnal insects), the insects feeding on *E. rubiginosa* appear similar at the higher taxa level than those feeding on other *Eperua* spp. in French Guiana (Gombauld, 1996), although species may be different. In particular, at least 16 species of chrysomelids (mostly Eumolpinae), nine species of Curculionidae (Entiminae), plus various species of moths (Geometridae and Tortricoidea, notably), and a Cecidomyiidae, which induces bud galls, feed on *Eperua* seedlings at Mabura Hill.

Leaf-cutting ants

All leaf-cutting ants are members of Attini of the subfamily Myrmicinae (Hymenoptera: Formicidae). The tribe include 190 species, confined to the nearctic and neotropical regions (Cherrett *et al.*, 1988). Weber (1949) gives detailed accounts of the biology of most species of leaf-cutting ants in Guyana, where eight genera are recorded: *Cyphomyrmex* (three species), *Myocepurus* (one species), *Myrmicocrypta* (six species), *Apterostigma* (six species), *Sericomyrmex* (five species), *Trachymyrmex* (nine species), *Acromyrmex* (four species) and *Atta* (three six species). However, the main species of leaf-cutting ants which harvest fresh vegetable substrates are species of *Atta* and *Acromyrmex* (Cherrett *et al.*, 1988). In the Guianas, three species of *Atta* are present (*A. cephalotes* L., *A. sexdens* L. and *A. laevigata* [Smith]) and four of *Acromyrmex* (*A. octospinosus* (Reich.), *A. landolti* (For.), *A. hystrix* (Latreille) *and A. coronatus* [F.]).

In the neotropical region, leaf-cutting ants have been considered to be 'dominant invertebrates' (Wheeler, 1907) and the most serious general insect pests of agriculture (Cherrett, 1968). They cut sections of leaves and, to a lesser extent, flowers and fruits, transport them to the nest chambers underground, where they excrete on them and inoculate them with a mutualistic fungus species, *Attamyces bromatificus* Kreisel (Basidiomycetes). This species of fungus has never been found outside the ant nests (Cherrett *et al.*, 1988). The ants feed on the fungus and discard all detritus into refuse dumps. The fungi require careful gardening to be retained in monocultures and garden temperatures are regulated. Large underground nests of *Atta* may be over 100 m^2 in surface area and include millions of individuals (Cherrett, 1982). Leaf-cutting ant colonies may be long-lived, often persisting for ten years or more (Cherrett, 1986). In Suriname, Stahel and Geijskes (1939, 1940, 1941) described the organization of the nest of *Atta cephalotes* and *A. sexdens*, while Geijskes (1953) observed nuptial flights of *Atta*.

Grazing damage due to leaf-cutting ants may be considerable and the ants attack a variety of crops (e.g. Buckley, 1982). In particular, citrus, cocoa, pastures and coffee suffer most and the nomadism of some Amerindian tribes is said to have been a response to upsurges in *Atta* populations after forest clearing (Cherrett, 1982). Average figures suggest that in tropical rainforests leaf-cutting ants may be harvesting 17% of total leaf production (Cherrett *et al.*, 1988). Cherrett (1972b) studied the substrate being carried into a nest of *A. cephalotes* in a forest near Bartica, Guyana. He estimated that during a 24 h period, approximately 700 g of fresh vegetable substrate was carried into the nest, about 60% of it as leaves, the rest being flowers. Ants carrying leaf fragments were significantly larger than ants carrying flower fragments. A general bibliography of leaf-cutting ants has been compiled by Cherrett and Cherrett (1989).

The biology of leaf-cutting ants has been best studied in Guyana by Cherrett and his co-workers (e.g. Cherrett, 1968, 1972a,b, 1980, 1982, 1983, 1986; Cherrett and Peregrine, 1976). Although leaf-cutting ants such as *A. cephalotes* defoliate a wide range of plant species, including some ant plants such as *Tachigali paniculata* (Wheeler, 1921), they forage selectively and

chap05.qxd 19/1/05 3:45 pm Page 309

the impact on particular plant species may be much greater than on the plant community as a whole (Buckley, 1982). For example, *A. cephalotes* tends to damage broad-leaved plants only, whereas *A. laevigata* cuts both grasses and broad-leaved plants (Cherrett, 1972a). Thorough studies of the foraging patterns of *A. cephalotes* by Cherrett, based on relatively long-term observations of a nest near Bartica in Guyana (e.g. Cherrett, 1968, 1972b; and see Cherrett *et al.*, 1988), showed that the ants are mostly nocturnal. *A. cephalotes* cut leaf sections from 36 out of 72 available plant species in the study area, concentrating on a few of these. Most foraging activity took place up to 30–45 m away from the nest and, in the canopy, above 12 m. The ants prefer young leaf material, flowers and buds, and, in particular, plant tissues both less tough and dense and those with high moisture. Plants are particularly at risk when flowering or flushing. The less dense the plant material, the more successful the small workers will be in cutting and carrying it back to the nest.

Several other studies led Cherrett and his co-workers (see references above) to conclude in substance that:

1. Whilst the interaction between leaf-cutting ants and the fungi that they cultivate is highly specialized, it is relatively unspecialized with regard to the use of plant species;
2. Only 5% of the energy requirements of an ant colony is provided by the fungus, the rest being supplied directly by plant sap; however, the fungus provides essential nutrients;
3. The outcome of the mutualistic relationship between the ants and the fungus is a most unusual degree of ecological dominance in diverse tropical vegetation, brought about by wide polyphagy; in short, both ant and fungus can utilize a far wider range of host plants than either could alone and, in doing so, they attain large population sizes (Cherrett *et al.*, 1988);
4. *A. cephalotes* has developed a conservative grazing system which prevents it from over-exploiting, and hence destroying, the vegetation in the area around the nest; and
5. The introduction of agriculture disrupts the pattern in (4) above, and may contribute to the pest status of this species.

Discussion

Although the overall body of published information on insect–plant interactions in the rainforests of the Guianas may appear considerable, it concerns mainly pollinators, leaf-cutting ants, ant gardens and other ant–plant interactions (Table 5.3). Most other interactions have been neglected, particularly those involving folivorous insects, including leaf-mining and gall-making species. Despite these caveats, it is of interest to discuss whether leaf and sap resources and insect–plant interactions in the Guianas may be different than at other, better studied locations in tropical rainforests. We concentrate on monodominance of tree species and host specificity of folivorous insects in order to extend the debate to the diversity of insect–plant interactions in the rainforests of the Guianas.

Monodominance of tree species and host specificity of folivorous insects

As emphasized elsewhere in this book, tree diversity in the rainforests of the Guianas depends mostly on local conditions such as soil type, drainage class and topographical features. Floristically-rich mixed forests tend to occur on well-drained soils, whereas on poorly-drained soils dominance of one or a few species of Leguminosae is commonplace. Typically, these monodominant stands exhibit a much lower vegetational diversity than mixed forests (e.g. Davis and Richards, 1933, 1934; ter Steege *et al.*, 1996). Monodominant species of Leguminosae are found in *Eperua*, *Mora*, *Dicymbe*, *Peltogyne*, *Dicorynia*, *Dimorphandra* and *Vouacapoua*. In addition, there is often a trend for certain species in genera such as *Chlorocardium*, *Carapa* (Meliaceae), *Eschweilera* spp. and *Lecythis* spp. (Lecythidaceae), *Catostemma*

chap05.qxd 19/1/05 3:45 pm Page 310

Table 5.3. Assessment of current scientific knowledge about particular insect–plant interactions in the Guianas, with an emphasis on rainforest insects.

Interaction	French Guiana	Suriname	Guyana
Pollination	XX	XX	X
Flower consumers	0	0	X
Seed predation	X	0	X
Seed dispersal	X	0	X
Sap-sucking insects	0	0	X
Herbivory	XX	0	X
Leaf-chewing insects	X	0	X
Leaf-cutting ants	X	X	XX
Extrafloral nectaries and food bodies	XX	0	X
Stem-boring insects	0	0	X
Ants nesting in stems	XX	0	XX
Ant gardens	XX	0	X
Phytotelmata	0	0	X
Wood-eating insects	XX	X	XX

0=nil, anecdotal, restricted or difficult to obtain.
X=some information available, sometimes unpublished.
XX=relatively extensive information.

spp., *Pentaclethra*, *Triplaris* (Polygonaceae), *Hura* (Euphorbiaceae) and *Alexa* (Papilionaceae) to achieve co-dominance locally in the Guianas (Whitton, 1962; ter Steege *et al.*, 1993; Forget, 1994).

What are the likely results of these mono- or co-dominance patterns for insect herbivores, particularly for free-living folivorous insects? Price (1992) considered the influence of the resource base on the community structure of tropical insect herbivores to be paramount. A review of the information available from different tropical locations showed that this is credible (Basset, 1996). The following hypotheses can be put forward, following Price's (1992) rationale:

1. Reduced vegetational diversity in monodominant stands may reduce local insect diversity (the number of available niches is likely to decrease, particularly in the canopy; see Connell and Lowman, 1989), but particular insect taxa may be rather specialized and diverse in monodominant stands, since both the resource base and the predictability of resources provided by monodominant stands may be high.
2. For various reasons, monodominant tree species may be unpalatable to insect herbivores; the low resource base provided by such trees may then locally promote low insect species richness and low numbers of specialist species.

Although both hypotheses overall predict reduced insect diversity, they differ with regard to insect–host specificity. What is the evidence? Only circumstantial data exist in order to approach this problem. One example worth mentioning pertains to aphids, which are less diverse than psyllids in tropical habitats. Dixon *et al.* (1987) convincingly explained differences in host use for tropical psyllids and aphids. Both groups are rather host-specific, but aphids are much shorter-lived than psyllids and, consequently, have more difficulties to disperse efficiently on their hosts in a mosaic of diverse tropical vegetation in comparison with psyllids. Aphids are well-represented on legumes (e.g. van Emden, 1972) and should be also relatively well-represented in monodominant legume stands in the Guianas, providing that their resource base is large enough (i.e. in this case, that their hosts are palatable enough). However, Beebe (1925) commented on the scarcity of

chap05.qxd 19/1/05 3:45 pm Page 311

aphids in the rainforests near Kartabo. Further, seedlings of the legumes *Eperua* spp., *Mora* spp. and *Pentaclethra macroloba* rarely support aphid species, but the two former genera often support high loads of psyllids (Gombauld, 1996; Basset and Charles, 2000). This observation suggests that monodominant stands may provide a low resource base for aphids, which is in support of hypothesis 2.

Forget (1992; see also Richards, 1996) suggested that chemical and structural defences in *Eperua* spp. leaves, in addition to understorey tolerance at all stages of development, are likely to participate in promoting tree dominance of this species group in the forests of the Guianas, consistent with hypothesis 2. As emphasized previously, monodominant stands occur mostly on nutrient-poor or poorly drained locations (e.g. Beard, 1946; ter Steege *et al.*, 1993). The leaves of slow-growing monodominant trees may not only be well-protected chemically and physically, they may also be relatively nutrient-poor (e.g. total nitrogen in sapling leaves of mono- or co-dominant species at Mabura Hill do not appear to exceed 1.8% of dry weight: Raaimakers *et al.*, 1994, Table 2.1). It is well-known that herbivores of nutrient-impoverished plants tend to be more polyphagous than those feeding on nutrient-rich plants (Mattson and Scriber, 1987). An analogous situation to that in the Guianas could well be the dominant forests of dipterocarps in South-east Asia, which are low in nutrients and support very few lepidopteran defoliators, most of them being polyphagous (Holloway, 1989). Data from Barro Colorado Island, Panama, also suggest that Membracidae feeding on slow-growing, shade-tolerant hosts are less diverse than those feeding on fast-growing hosts, but, consistent with hypothesis 1, they appear to be rather specialized (Loye, 1992).

Further, many species in several insect groups (e.g. Acridoidea, Fulgoroidea, Membracidae, Cerambycidae, Scolytidae, Platypodidae, Hesperiidae, etc.) appear to exhibit a relatively wide geographical distribution, unconfined to the Guiana Shield. Generalist insect herbivores tend to be larger than specialists, and larger herbivores tend to have a wider geographical range (e.g. Gaston and Lawton, 1988). Thus, a wide geographical range of many species of insect herbivore would tend to support hypothesis 2. An alternative explanation is that insects are relatively specialized (monophagous or oligophagous), but their hosts are widely distributed. De Granville (1988) considered that about 35% of plant species (within certain plant taxa) are endemic to the Guianas. Further, many mono- or co-dominant species present in the Guianas are near-endemic and do not extend much beyond that region (e.g. ter Steege, 1990). For example, Nascimento and Proctor (1994) commented that monodominant stands are rare in Brazil (for example, *Peltogyne gracilipes* on Maracá Island). Thus, the relatively high level of endemism of several tree species in the Guianas would not suggest a pattern of high level of insect specialization on widely distributed host trees in Amazonia.

Overall, there appears to be more circumstantial evidence to accept hypothesis 2, although hypothesis 1 may be more appropriate for certain insect taxa. However, at present, we are reluctant to accept hypothesis 2 before two further points can be clarified. First, tropical insects which have been formally identified and whose geographical range can be inferred are more likely to be better known generalists, these often being insect pests. Although there has been speculation over the tremendous local endemism in Amazonian canopy insects (e.g. Erwin, 1983), the impression of high insect endemism in the lowland tropics may be merely a consequence of poor sampling (e.g. Gaston *et al.*, 1996). For example, before exchanging information with his colleagues in French Guiana, the present first author thought that the lycaenid *Thestius pholeus* was relatively specialized, feeding on *Catostemma* at Mabura Hill, Guyana. In fact, this species also feeds on *Vouacapoua* in French Guiana, with apparent host-specificity (Joly, 1996). This case of apparent local specialization, but with rather

chap05.qxd 19/1/05 3:45 pm Page 312

polyphagous habits over the entire geographic range of the species, has been documented in several cases (e.g. Fox and Morrow, 1981) and may indeed be relatively common in tropical insect herbivores (e.g. Janzen, 1981). Further, poor sampling increases the difficulty of recognizing morphological variation associated with many widespread species (Gaston *et al.*, 1996).

Secondly, most insect collecting in the Guianas has been from the understorey. The abundance and the diversity of insect herbivores are typically higher in the canopy of rainforests than in their understorey, because, as can be again argued, the resource base is higher in the former (e.g. Basset *et al.*, 1992, 1999, 2003). Similarly, understorey insects may be less specialized (and have a wider geographical range) than in the canopy. We have limited evidence that some free-living insects feeding on seedlings in the understorey appear to be rather generalist (Gombauld, 1996; Basset, 1999).

In summary, we believe that future studies upon the host-specificity of insect herbivores foraging in the canopy will help greatly to evaluate whether hypothesis 2 is generally correct and not an artefact of the limited information presently available. These studies should be supported by adequate sampling effort (sufficient numbers of insects collected from sufficient numbers of host plants) and adequate taxonomic effort.

Diversity of insect–plant interactions in the rainforests of the Guianas

It is well-known that mammalian diversity in Amazonia is least in the Guiana subregion (Voss and Emmons, 1996). What of insect–plant interactions, and particularly insect herbivores, in this regard? First, entomological knowledge in arguably the best studied of the three Guianas, Guyana, is notoriously low (e.g. Munroe, 1993; Funk, 1997) and this greatly impedes analyses of host specificity and endemism. Second, generalizations are difficult since, for example, patterns of mammalian diversity do not follow those of butterflies worldwide (Robbins and Opler, 1997). Third, patterns may be dissimilar for different insect taxa belonging to different feeding guilds. For example, whereas folivorous insects could be less diverse in monodominant stands (see discussion above), bee diversity appears to be poorer in diverse forests (Roubik, 1990). Flowers represent a much less protected resource, both physically and chemically, than leaves and, as such, patterns of host use may well be very different between respective insect feeding guilds using these different resources.

There are no suitable data (i.e. sample size large enough and comparable in different locations) to compare the fauna of insect herbivores in the Guianas with those elsewhere, particularly in Amazonia. However, it may be argued that the interactions in ant gardens are clearly less diverse in the Guianas than in Peru (Davidson, 1988). Further, circumstantial evidence suggests that the diversity of insects, particularly of herbivores, may indeed be relatively low in the Guianas. For example, Tavakilian (1993) concluded, from extensive observation, that light trapping of Coleoptera in French Guiana yields poorer results than in Africa or Asia. Incidentally, the present first author was also surprised at the low occurrence, all-year long, of insects attracted to light at Mabura Hill, Guyana, in comparison with other locations in the tropics.

Further, leaf-cutting ants are abundant in the neotropical region and common in the Guianas. Yet, despite this, leaf damage in the rainforests of the Guianas appears relatively low in comparison with elsewhere in the tropics (see Coley and Aide, 1991). This might be a consequence of low grazing rates on leaf resources low in nutrients, or an indication of the low abundance and diversity of insect herbivores other than leaf-cutting ants. It is well known that forests growing on nutrient-poor white sands, for example, are less prone to attack by free-living insect herbivores (e.g. Janzen, 1974). The data of Isaacs *et al.* (1996) in Guyana indeed suggest that apparent leaf damage unrelated to leaf-cutting ants amounted to about 5%, a rather low value.

chap05.qxd 19/1/05 3:45 pm Page 313

However, care must be exercised in this type of extrapolation, since it is notoriously difficult to relate insect abundance and diversity to apparent leaf damage (e.g. Marquis, 1991; Basset and Höft, 1994).

These patterns of relatively low diversity, if actually correct, may be partly related to monodominance of certain host plants, as discussed previously for folivorous insects. Since monodominance patterns may increase with respect to soil types from the series French Guiana–Suriname–Guyana, to culminate in the latter country, it would be interesting to test whether the diversity of particular insect taxa also decrease along this series, as more and better data become available. One related question would be to assess local differences in insect species richness between well-drained and poorly drained forests. The extent of structural and vegetational differences in these two habitats is such (e.g. ter Steege *et al.*, 1993) that this is likely to affect many taxa of insect herbivores. For example, De Dijn (2004) reported such differences for bee assemblages in Suriname.

To conclude, it is clear that there are severe gaps in our knowledge of insect–plant interactions in the Guianas. We believe that it may be difficult, if not futile, to discuss possible patterns and speculate further beyond that which we have suggested above without additional data. We hope that this review will stimulate entomologists and ecologists to undertake much needed studies of insect–plant interactions in the rainforests of the Guianas. The Guianan Shield, with its unique large and often undisturbed forest formations, including some peculiar monodominant stands, represents a potential wealth of information for scientists, which may challenge some commonly held views in tropical ecology. Our immediate responsibilities are to study thoroughly these habitats before they disappear, and to conserve most of them for future generations.

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chap05.qxd 19/1/05 3:45 pm Page 314

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chap05.qxd 19/1/05 3:45 pm Page 315

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chap05.qxd 19/1/05 3:45 pm Page 316

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chap05.qxd 19/1/05 3:45 pm Page 317

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chap05.qxd 19/1/05 3:45 pm Page 318

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chap05.qxd 19/1/05 3:45 pm Page 319

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chap05.qxd 19/1/05 3:45 pm Page 320

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