HOST USE BY CHRYSOMELID BEETLES FEEDING ON MORACEAE AND EUPHORBIACEAE IN NEW GUINEA

VOJTECH NOVOTNY[1], YVES BASSET[2], G.A. SAMUELSON[3]
and SCOTT E. MILLER[4]

[1]*Institute of Entomology, Czech Academy of Sciences and Biological Faculty, University of South Bohemia, Branisovska 31, 370 05 Ceske Budejovice, Czech Republic, novotny@entu.cas.cz;* [2]*Smithsonian Tropical Research Institute, Apartado 2072, Balboa, Ancon, Panama, bassety@tivoli.si.edu;* [3]*Bishop Museum, Dept of Natural Sciences, 1525 Bernice Street, Honolulu 96817-0916, U.S.A., alsam@bishop.bishop.hawaii.org;* [4]*Biodiversity and Conservation Programme, International Centre of Insect Physiology and Ecology, Box 30772, Nairobi, Kenya, scottm@bishop.bishop.hawaii.org*

Abstract

The composition and host specificity of chrysomelid communities, feeding on 15 species of Moraceae and 15 of Euphorbiaceae in New Guinea is detailed. All 30 plant species were trees or shrubs, growing in rainforest and coastal habitats. Chrysomelids were collected alive and tested in the laboratory for feeding on the plant species from which they were obtained. Only specimens which fed were considered in the analyses. Sampling spanned almost over three years and 9,186 individuals from 93 species, belonging to 5 subfamilies were collected. Eumolpinae and Galerucinae dominated in terms of abundance and species richness. The foliage-feeding community consisted almost exclusively of adults, as eumolpine and most of the galerucine larvae were probably root-feeders. Species richness of chrysomelid communities varied from 1 to 27 species per host plant species, and abundance from 8 to 1,462 individuals. Trees without diverse chrysomelid communities were fed upon mostly by generalists, whilst high density chrysomelid communities were dominated by specialists. Usually, Galerucinae were more host specific than Eumolpinae, but the overall host specificity of chrysomelids was rather low. In particular, there was a large overlap in the chrysomelid communities among congeneric plants. Most of the chrysomelid species fed on several congeneric hosts and were not strict monophages. Within *Ficus*, where such evaluation was possible, the similarity of chrysomelid communities did not reflect phylogenetic relationships among the host plants. Considered across plant genera, specialisation to a single genus was the most frequent case. Plant palatability, estimated from feeding experiments using a generalist species of weevil, was negatively correlated with the average host specificity in the chrysomelid community supported by this plant species; polyphagous chrysomelid species tended to be concentrated on palatable hosts. In conclusion, the patterns of host use by Eumolpinae and Galerucinae appear to be shifted towards oligophagy, in comparison with most of other subfamilies, feeding on Temperate herbs. Low host specificity of adults feeding on the foliage may be caused by the predominance of species with root-feeding larvae, and may explain the importance of plant palatability for the composition of chrysomelid communities.

1. Introduction

Many species of Chrysomelidae are distributed in the tropics and represent conspicuous elements of the fauna of tropical rain forests. Undoubtedly, one of the most significant issues when discussing the host specificity of insect herbivores such as the Chrysomelidae is the extent of specialisation of the numerous species that thrive in tropical rain forest and, particularly, that of species feeding in the canopy (Farrell and Erwin, 1988; Jolivet and Hawkeswood, 1995).

Perhaps with the notable exceptions of *Eucalyptus*- and *Salix*-feeding chrysomelids (for example, Ohmart, 1996; Rank *et al.*, 1996), the host ranges of species feeding on trees appear to be less well known than those feeding on herbs, particularly in the tropics. In part, this may have resulted from the relative ease of collection and observation of chrysomelids feeding on herbs, in contrast with the same of live specimens from trees. In the tropics, few studies of host specificity of tree-feeding chrysomelids have been conducted, particularly at the community level. For example, Basset and Samuelson (1996) presented some data on the host specificity of species found on ten distantly-related tree species in Papua New Guinea. Flowers and Janzen (1997) listed feeding records for Costa Rican chrysomelids, with many species feeding on trees.

Earlier studies of insect-plant interactions in the Temperate zone showed that, in general, trees support more species of insect herbivores than herbs, due to their higher architectural complexity (for instance, Lawton and Schröder, 1977). Although this observation has not been tested for Chrysomelidae in particular, it is probable that tropical trees may often harbour more species of chrysomelids than tropical herbs.

The host specificity of tropical species that belong to subfamilies such as the Hispinae, Cassidinae, Chrysomelinae, or Sagrinae is reasonably well-known and often appears to be rather narrow (for example, Gressitt, 1959; Jolivet and Petitpierre, 1976; Strong, 1977; Jolivet, 1989; Jolivet and Hawkeswood, 1995). For instance, Hispinae appear to be often associated with Monocotyledons (for instance, palms, *Heliconia*, etc.), Cassidinae with Convolvulaceae, while Chrysomelinae feed collectively on many plant families, but each species is rather specialised (Jolivet and Hawkeswood, 1995). However, the dominant chrysomelid groups in the canopy of tropical rain forests are often the Eumolpinae, Galerucinae and Alticinae (Farrell and Erwin, 1988; Basset and Samuelson, 1996). The host specificity of these groups in particular is poorly known; the host ranges of especially the first two subfamilies appear also to be more varied, involving both specialists and generalist of various degree (Jolivet and Hawkeswood, 1995). New data on the host specificity of these groups, and their communities feeding on tropical trees in particular, is necessary for analysis of the host specificity of Chrysomelidae.

Any study of host specificity greatly depends on the scale of the analysis, particularly on the identity and phylogenetic relatedness of the host plants being considered. The study of chrysomelids from numerous, closely related, co-occurring species of trees in rain forests could be informative, particularly with reference to problems such as the patterns of species packing of insect herbivores, and the maintenance of their diversity on the local scale. In Temperate ecosystems, studies on many related, for instance congeneric, plants are usually possible only using herbaceous species. Yet, in the tropics, they have been rarely attempted (but see Marquis, 1991, for such data on weevils). For instance, the above cited studies on chrysomelids in Papua New Guinea (Basset and Samuelson 1996) and Costa Rica (Flowers and Janzen 1997) included a selection of phylogenetically rather distant hosts. Tropical studies on closely related plants are indispensable since we want to know whether trees in the tropics support a rather specialised chrysomelid fauna, perhaps depending on the chemical characteristics of the host, as is known for the chrysomelids feeding on certain herbs in the Temperate zone (for instance, Tahvanainen, 1983).

Given the number of both chrysomelid and plant species in the tropical rainforest, dissecting pair-wise interactions one by one is not a feasible proposition. Instead, broader-based studies, searching for general patterns in herbivore communities on a wide array of

host plants may represent a more promising approach to the study of tropical communities. Numerous plant traits, potentially important for chrysomelid host choice, exist. The challenge is to identify those which are important for a wide range of chrysomelid species on a variety of plants, thus having a pervasive influence on the structure of the whole chrysomelid community on the diverse tropical vegetation. It is argued here that plant palatability for generalist herbivores might be one such generally-important trait. Plant palatability is a composite result of the plant's qualities and its herbivores' preferences, so it may differ from one plant-herbivore interaction to another. However, there is an interesting possibility that while specialists are, by definition, idiosyncratic, generalists may respond similarly to certain plant qualities, making some plants generally palatable or impalatable to them (Cates and Orians, 1975; Grime, 1979; Price, 1991; Herms and Mattson, 1992). If this were found to be so, the palatability for generalists might become a good predictor of at least the generalist part of herbivorous communities.

The present contribution details information about the composition and host specificity of chrysomelid communities, feeding on 30 tree and shrub species from the Moraceae and Euphorbiaceae in the Madang area of Papua New Guinea. It concentrates on the host specificity of chrysomelids, and the importance of plant palatability and their phylogeny (or taxonomic classification) on the structure of chrysomelid communities. This study of a fraction of plants potentially available to chrysomelids in a single rain forest ecosystem is a small step towards understanding the host specificity of chrysomelids feeding on tropical trees and it is hoped that it will stimulate similar studies at other tropical locations, and in different types of rain forests.

2. Methods

2.1. Study area and insect sampling

The study area was situated in the Madang province of Papua New Guinea and was delimited as part of the lowlands (0-400m asl), stretching from the coast to the slopes of the Adelbert Mts, which lie between the Gogol and Sempi Rivers. This approximate rectangular area of 17 x 31 km encompasses about 434 km² of primary and secondary forests, 21 km² of coastal habitats (including seashore and ruderal vegetation in coconut plantations) and the town of Madang. Field work was concentrated in primary and secondary lowland forests near Baitabag, Ohu and Mis Villages, and in a coastal area near Riwo village (145°41-8' E, 5°08-14' S). The average annual rainfall in the Madang area is 3,558 mm, with a moderate dry season from July to September, mean air temperature is 26.5 °C which varies little throughout the year (McAlpine *et al.*, 1983).

Chrysomelid beetles were collected from the foliage of trees individually, by hand. Taller trees were often climbed into, or only lower, accessible branches were examined. Insects were sampled by five collecting teams usually including three people per team. Insect collecting continued from July 1994 to March 1996 on 15 species of *Ficus* and from August 1996 to August 1997 on 15 species of Euphorbiaceae.

Sampling effort was recorded as the time spent searching the foliage of each of the plant species for insects, which was approximately proportional to the leaf area examined. The number of tree inspections, that is, a particular tree sampled at a particular time, was also

recorded. Overall, the sampling programme, which surveyed individual trees in a variety of age classes and growing in various habitats, was optimised towards the estimation of the total number of chrysomelid species feeding on each of the tree species studied. For species of *Ficus*, collecting effort varied from 22.9 to 25.6 hours (average 24.7 hours per species), while for all Euphorbiaceae it amounted to exactly 24.7 hours per species. The total number of tree inspections was 25,152. This sampling effort represented approximately 950 days of field work.

In the laboratory, each chrysomelid was provided with fresh, as far as possible young, foliage of the plant species it was collected from and kept on it until it fed or died. Only the specimens which fed were considered in the analyses, to exclude transient species from the samples. All insects were assigned to morphospecies and identified as far as possible. Voucher specimens are deposited in Bishop Museum, Honolulu.

2.2. Host plants

Thirty locally abundant species of trees and shrubs, involving 15 species of *Ficus* (Moraceae), 6 species of *Macaranga* and 9 species representing 9 other genera of Euphorbiaceae, were selected for the study of their chrysomelid fauna (Table 1). Moraceae and Euphorbiaceae, with 3,000 and 5,000 species worldwide respectively (Heywood, 1993), were selected for the study since they represent important components of tropical floras (for instance Gentry, 1990). They are also abundant and species-rich in the Madang area, as well as in other lowland rain forests in New Guinea (for instance, Oatham and Beehler, 1998).

Ficus is an exceptionally large, pantropical genus, with over 700 species (Berg, 1989). New Guinea is one of the main centres of its diversity with 135 described species (Corner, 1965). In the lowlands around Madang, there is at least 48 species of *Ficus* (G. Weiblen, pers. comm.), from which 15 were selected for the present study. This selection included one monoecious strangling fig (*F. microcarpa*) and 14 gynodioecious free standing trees and shrubs. A cladistic analysis, using molecular and morphological characters (G. Weiblen, pers. comm.), did not confirm the monophyly of all Corner's (1965) species series. The results of this analysis were used to classify the present species to monophyletic groups (Table 1A).

Both in PNG (Höft, 1992) and in the Madang area (pers. obs.), Moraceae other than *Ficus* are of lesser importance in terms of species richness and biomass (with the exception of *Artocarpus*). Thus, the following data on insects feeding on *Ficus* may be used to study the local distribution of leaf-chewing insects on the family Moraceae.

There are 461 species of Euphorbiaceae reported from New Guinea, 73% of them being endemic (van Welzen, 1997). *Macaranga*, with over 280 species distributed from West Africa to the islands of the western Pacific, is by far the largest genus of early successional (pioneer) trees in the world (Whitmore, 1979). New Guinea is the main centre of diversity for this genus, with 82 species described (van Welzen, 1997) and some more awaiting description. [It should be noted that the discovery of 2 new species (Whitmore, pers. comm.) resulted from the present study alone]. The six species of *Macaranga* studied belong to the three largest species groups, of the nine present in New Guinea (Whitmore, 1980).

The other nine species of Euphorbiaceae, one per genus, included representatives of

Table 1. Host plants studied.

A) *Ficus* spp.

Code	Species	Phy.	Pal.	Habitat
BE	*Ficus bernaysii* King	2.2	0.10	primary forest
BO	*Ficus botryocarpa* Miq.	2.2	0.09	secondary forest
CO	*Ficus conocephalifolia* Ridley	2.1	0.10	primary forest
CP	*Ficus copiosa* Steud.	2.1	0.24	secondary forest
DA	*Ficus dammaropsis* Diels	2.2	0.52	secondary forest
H1	*Ficus hispidioides* S Moore	2.2	0.05	secondary forest
MI	*Ficus microcarpa* L. f.	1	0.00	sea coast
NO	*Ficus nodosa* Tejsm. & Binn.	2.2	0.24	secondary forest
PH	*Ficus phaeosyce* Lauterb. & K. Schum.	2.1	0.19	primary forest
PU	*Ficus pungens* Reinw. ex Bl.	2.2	0.13	secondary forest
SE	*Ficus septica* Burm. f.	2.2	0.00	secondary forest
TI	*Ficus tinctoria* G. Forst.	2.1	0.09	sea coast
TR	*Ficus trachypison* K. Schum.	2.1	0.13	secondary forest
VA	*Ficus variegata* Bl.	2.2	0.44	secondary forest
WA	*Ficus wassa* Roxb.	2.1	0.25	secondary forest

B) Euphorbiaceae spp.

Code	Species	Tax.	Pal.	Habitat
MA	*Macaranga aleuritoides* F. Muell.	1.1.a	0.69	secondary forest
MB	*Macaranga brachytricha* Airy Shaw	1.1.b	0.63	secondary forest
MD	*Macaranga densiflora* Warb.	1.1.c	0.70	secondary forest
MQ	*Macaranga quadriglandulosa* Warb.	1.1.c	0.62	secondary forest
M2	*Macaranga* sp. nov. 2 (Whitmore, in litt.)	1.1.c	0.88	primary forest
M3	*Macaranga* sp. nov. 3 (Whitmore, in litt.)	1.1.c	0.70	secondary forest
BR	*Breynia cernua* (Poir.) Muell. Arg.	4	0.00	secondary forest
CD	*Codiaeum ludovicianum* Airy Shaw	2	0.11	rocky river beds
EN	*Endospermum labios* Schodde	2	0.58	secondary forest
EX	*Excoecaria agallocha* L.	3.1	0.08	sea coast
HO	*Homalanthus novoguineensis* (Warb.) K. Schum	3.1	0.26	secondary forest
ML	*Mallotus mollissimus* (Geiseler) Airy Shaw	1.1	0.62	secondary forest
ME	*Melanolepis multiglandulosa* (Reinw.ex Bl) Rchb.&Zoll	1.2	0.16	secondary forest
PH	*Phyllanthus lamprophyllus* Muell. Arg.	4	0.62	rocky river beds
PI	*Pimelodendron amboinicum* Hassk.	3.2	0.11	primary forest

Phy. – monopyletic groups, based on a cladistic analysis of morphological and molecular characters (Weiblen, pers. com.); Tax. – taxonomic classification; numbers refer to subfamily.tribe: 1 – Acalyphoideae (1 - Acalypheae, 2 – Chrozophoreae), 2 – Crotonoideae 3 – Euphorbioideae (1 – Hippomaneae, 2 - Stomatocalyceae), 4 – Phyllanthoideae; letters refer to species groups in *Macaranga*: a – longistipulata, b – tanarius, c – dioica; Pal. – palatability (see Methods).

four, of five, subfamilies of Euphorbiaceae recognized by Webster (1975). No cladistic analysis is available for all the genera in our study. Therefore, we have used the recent suprageneric classification of Euphorbiaceae (Webster, 1975) and the classification of species groups in *Macaranga* (Whitmore, 1980) as surrogates for phylogeny (Table 1B). The placement of three genera related to Hippomaneae in a more recent phylogenetic analysis (Esser and van Welzen, 1997) agrees with that in the Webster's classification.

2.3. Host specificity

The host specificity of each species was quantified by Lloyd's index, which characterises the variance of a species' distribution among the 30 plant species studied (Lloyd, 1967; see also Lepš, 1993). Its value is minimum for an equitable distribution (that is, indiscriminate polyphagy) and increases with increasing host specificity. Many species were too rare to derive any estimates of their host specificity with confidence. Potentially spurious correlation of host specificity, expressed by Lloyd's index, on species abundance (that is, sample size) disappeared once species collected as less than 15 individuals were excluded from the analysis. This threshold was used to divide species into those common and rare; all analyses concerning host specificity were based on the former only.

Lloyd's index may be influenced by imbalanced choice of host plants in the present study, which include many species of *Ficus* and *Macaranga*, but only a single species from any other genus. Species indiscriminately polyphagous with respect to congeneric plants, but restricted to a single plant genus would thus attain very different values of Lloyd index, dependent on the genus on which they were specialised. Thus, host specificity was characterised also by the number of host plant genera used by a chrysomelid species. All common species were further classified into specialists (at least 90% of individuals concentrated on a single host plant genus) and generalists (remaining species).

Overall host specificity in a chrysomelid community feeding on a particular tree species was quantified as the average Lloyd's index and the average number of host genera for an individual chrysomelid feeding on a given tree species. These characteristics are averages of the Lloyd's index and the number of host genera, respectively, weighted by species abundance. Again, only common species of chrysomelids were used for the calculations.

The average number of host plants per chrysomelid species appeared to be the most straightforward characteristic of the host specificity in the entire chrysomelid community. However, the number of host plants recorded for a chrysomelid species is determined by its host specificity as well as its abundance. Obviously, the number of hosts may be underestimated severely for rare species. In order to separate host specificity from abundance, the number of hosts was calculated only for the species collected as at least 15 individuals from the set of plant species considered.

Host plant is defined either as a plant suitable for the completion of the herbivore's life cycle, or a plant fed upon by at least one of the herbivore's developmental stages. The latter meaning was used throughout this study as virtually all host plant records concerned feeding by adults, while feeding preferences by their larvae remained unknown.

2.4. Plant palatability

Highly generalist weevils (*Oribius* sp., species CURC012) were starved for 24h and then placed on potted saplings of the tree species studied. Each weevil was introduced inside a plastic vial which contained one leaf *in situ*. Feeding damage was scored visually after 24h on a logarithmic scale, as follows: 0 – no feeding; 1 – attempting to feed; 10 – moderate feeding; 100 – extensive feeding. During these experiments, two to five saplings were used for each plant species. On average, the feeding damage of 25 different weevils was measured for each plant species. An index of palatability was derived by recording the number

of cases in which a score of 100 was attributed, divided by the number of cases tested. This procedure emphasised regular feeding as compared to food-probing.

2.5. Statistical analyses

The similarity in the composition of chrysomelid communities was analysed by the agglomerative cluster analysis (Ward's method) and by direct (Canonical Correspondence Analysis, CCA) and indirect (Correspondence Analysis, CA) ordinations, using the Euclidean distance on $\log_{10}(N+1)$ transformed data. The CCA relates the composition of samples to environmental variables. Palatability was used as the sole environmental variable in order that the first (constrained) ordination axis was constructed to maximise fit between tree palatability and the composition of its chrysomelid communities. The CCA score on this axis, obtained for each chrysomelid species, represents a species' optimum with respect to the host plant palatability. The remaining (unconstrained) axes capture residual variation in the species data after extracting the constrained axis. The CA orders samples only on the basis of their species composition; environmental variables, such as palatability, are only correlated with the ordination axes *a posteriori*, reflecting the sample composition. The Canoco 4.0 and CanoDraw 3.1 software was used for the ordinations.

The species and singleton accumulation curves were calculated as the average from 100 replicates, each accumulating samples in a random sequence.

3. Results

3.1. Taxonomic composition

The sampling produced 9,186 individuals of chrysomelids with confirmed ability to feed on the plant species from which they were collected. Almost all of these individuals were adults; larvae of only *Atysa* and *Sastra* spp. were found freely feeding on the foliage. In total, 93 species from five subfamilies were collected (Appendix 1). The only two important subfamilies were Eumolpinae (45 spp., 6,977 individuals) and Galerucinae (37 spp., 2,023 individuals), together accounting for 88% of species and 98% of individuals. Eumolpinae species fed both on *Ficus* and Euphorbiaceae (171 and 164 host plant records, respectively), while Galerucinae were more concentrated on *Ficus* hosts (83 host plant records, vs. 36 on Euphorbiaceae; the difference between subfamilies was significant, $P<0.01$, Fisher's exact test).

Eumolpinae were less host specific than Galerucinae. For common species, the median number of host plants was 10 in eumolpines and 5 in galerucines, the number of host genera 4 and 1, and Lloyd's index 5.9 and 18.4, respectively (all differences significant, $P<0.05$, Mann-Whitney tests, n=38 species).

3.2. Host specificity

Many species were found as only a few individuals (20 species as singletons), so that their host range could not be estimated. The profound effect of insect abundance on their appar-
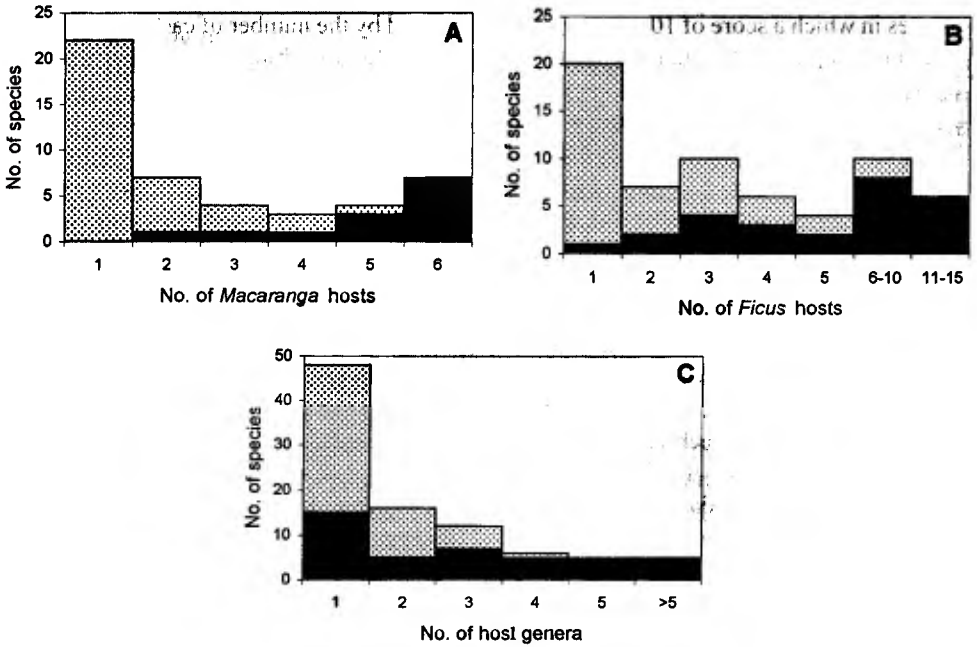
Fig. 1. Host specificity of chrysomelids on *Macaranga* spp. (A), *Ficus* spp. (B) and the whole set of studied tree species (C).
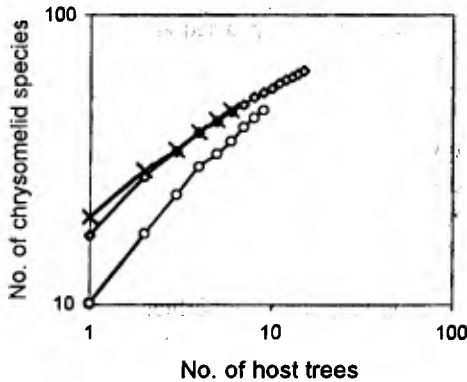Black – common species, stippled – rare species.

Fig. 2. Accumulation of chrysomelid species with increasing number of plant species studied.
Diamonds – *Ficus* spp., crosses and thick line – *Macaranga* spp., circles – Euphorbiaceae other than *Macaranga*.

ent host specificity is obvious from the number of hosts recorded for rare and common species (Fig. 1). Clearly, the prevalence of apparently monophagous species is caused by the rare species. Data for common species indicate a large overlap in their chrysomelid fauna among congeneric plants. This is particularly true for *Macaranga*, where the modal host specificity was polyphagy on all species studied and the average was 5.1 host species (Fig. 1a). Similar trends can be seen in *Ficus*, where the average was 7.0 hosts per chrysomelid species (Fig. 1b). In contrast, the specialisation to a single genus appeared to be
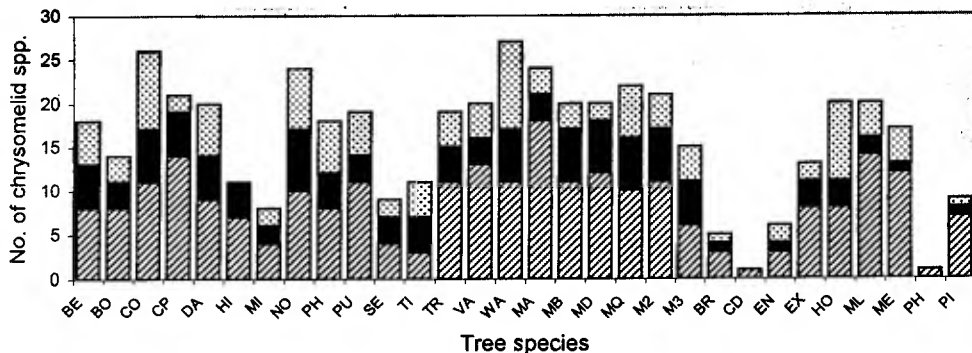
Fig. 3. Species richness of chrysomelids on various species of *Ficus* and Euphorbiaceae.
Hatched - generalists, black - specialists, stippled - rare species; see Table 1 for full names of host plants.

most common in the whole data set, and the average was only 3.0 host genera (Fig 2c). Despite such specialisation, the overlap between the chrysomelid fauna on Moraceae and Euphorbiaceae was not negligible, as 23 out of the 42 common species used hosts from both families.

The species accumulation curves (Fig. 2) indicate that the average number of chrysomelid species found on a tree from either of the two exceptionally large genera, *Ficus* and *Macaranga*, is higher than the average number for the remaining 9 genera. The slope of log (number of species) on log(number of hosts) regression with a 95% confidence interval was 0.46 (0.42 – 0.50) for *Ficus*, 0.37 (0.28 – 0.47) for *Macaranga*, and 0.73 (0.65 – 0.81) for Euphorbiaceae other than *Macaranga* (Fig. 2). This indicates that the rate of species accumulation with increasing number of tree species was slower for congeneric trees than for those from different genera, but all three accumulation rates were very high.

3.3. Abundance of generalists and specialists

The species richness of chrysomelid communities varied from one species (*Codiaeum* and *Phyllanthus*) to 27 species (*F. wassa*). Their composition in terms of specialists, generalists, and rare species is depicted in Fig. 3. There was a positive correlation between the number of specialists and generalists (r=0.473, P<0.01, n=30 trees) so that both groups contributed to an exceptionally high (or low) species richness on certain trees.

The abundance of chrysomelids on different tree species varied from 8 (*Codiaeum*) to 1,462 (*Excoecaria*) individuals. There was a well-defined group of plant species with low abundance of chrysomelids (less than 100 individuals), most of which (>90%) were generalists (*Codiaeum, Endospermum, Phyllanthus, Pimelodendron, Melanolepis*). For the remaining trees, the proportion of specialists was increasing with the abundance of their chrysomelid community (Fig. 4). *Mallotus*, with a large chrysomelid community, composed mostly (99.5%) by generalists, is a notable exception to this trend. This is because its chrysomelid fauna overlaps with that of closely related *Macaranga* (see below). From the viewpoint of chrysomelids, *Macaranga* and *Mallotus* probably constitutes a single host genus. If this is accepted and the *Macaranga* and *Mallotus* amalgamated to a single data point, a very close relationship between the proportion of specialists and the abundance of
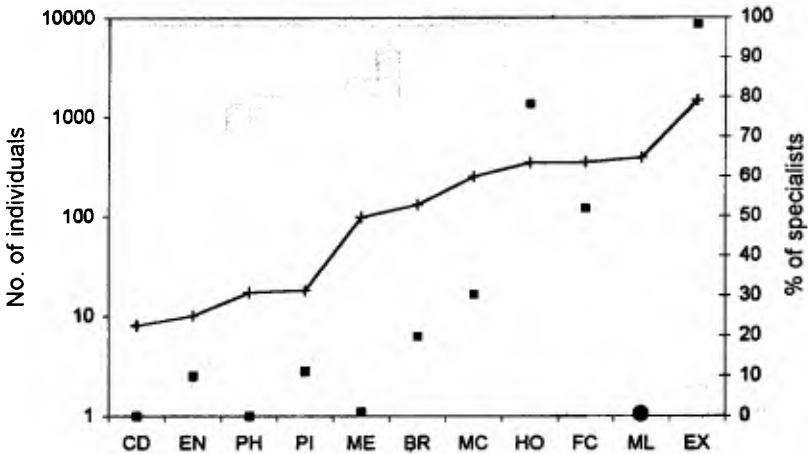
Fig. 4. Abundance of chrysomelids (line, left y axis) and the proportion of specialized individuals (squares, right y axis) on various plant genera.
FC – *Ficus*, MC – *Macaranga*; see Table 1 for other generic names.

chrysomelids across host plant genera ensues (r= 0.852, P<0.01, n=10).

Although the 22 specialist and 20 generalist species did not differ from each other in abundance (geometric mean 88 and 96 individuals per species, respectively; P>0.6, t-test), the 4,157 generalist chrysomelids were spread among 257 chrysomelid-host plant combinations, while the 4,844 specialists among only 108 such combinations. That suggests the largest chrysomelid populations feeding on a particular host belonged mostly to specialist species. Indeed, 8 from the 10 most abundant chrysomelid-plant combinations involved specialists.

The most abundant species, found as more than 500 individuals, were *Rhyparidella sobrina* (Bryant) gr. (a specialist on *Ficus*), *Rhyparida coriacea* Jacoby (a generalist), *Stethotes lateralis* Baly (a generalist), an unidentified galerucine sp. and *Rhyparida* sp. (both specialists on *Excoecaria*), and *Rhyparida huona* Gressitt (a generalist). The two specialists on *Excoecaria* also represent the two most abundant species-plant combinations.

3.4. Similarity of communities from different hosts

Cluster analysis separated the 13 forest species of *Ficus* and the rest of the data, which was, in turn, divided into a cluster involving all coastal species (*F. tinctoria, F. microcarpa* and *Excoecaria*), and a cluster of the forest Euphorbiaceae. The coastal species were further split into *Ficus* spp. and *Excoecaria*. The cluster of Euphorbiaceae was split into the *Macaranga* & *Mallotus* cluster and another, containing the remaining 8 species (Fig. 5). Further division of neither the forest species of *Ficus*, the *Macaranga* and *Mallotus* group, nor the other genera reflected their phylogenetic (or taxonomic) relationships (cf. Table 1). However, the only two plants from the riverine habitat (*Codiaeum* and *Phyllanthus*) formed a separate cluster.
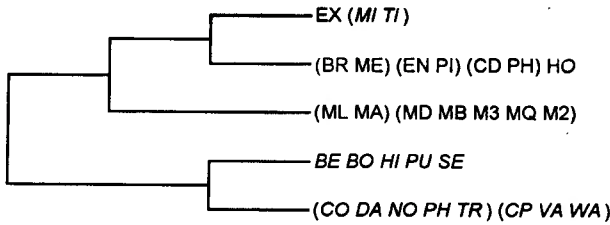
Fig. 5. Cluster analysis of chrysomelid communities from various host plants.
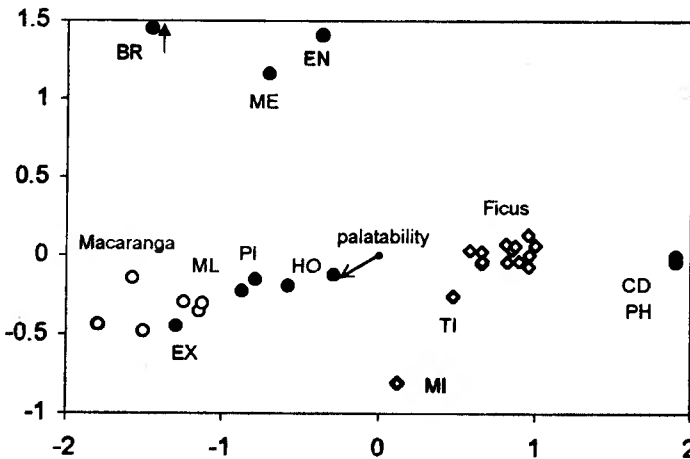*Ficus* hosts in italics; see Table 1 for full names of host plants.

Fig. 6. Correspondence analysis of chrysomelid communities from various host plants.
Each point represents a chrysomelid community from one plant species. Palatability depicted as a passive environmental variable. Diamonds – *Ficus* spp., empty circles – *Macaranga* spp., solid circles – other euphorb species. See Table 1 for full names of host plants.

The CA analysis revealed a compact cluster of the 13 forest species of *Ficus*, with the 2 coastal fig species nearby (Fig. 6). *Macaranga* spp. were close to each other, but the spread of the other Euphorbiaceae was wide. The two riverine species were again close to each other. These results suggest that two factors, *viz.* plant taxonomy, especially at suprageneric levels, and plant habitat, are important in shaping the composition of chrysomelid communities.

3.5. Plant palatability and chrysomelid host specificity

Plant palatability was negatively correlated with the average host specificity of chrysomelids feeding on them. This relationships was found both for Lloyd's index (r=-0.514, P<0.01, Mann-Whitney test, n=30 trees) and the average number of host genera (r=0.551, P<0.01). This result suggests that palatable plants are preferably fed upon by generalists, and *vice versa*. Consistent with this pattern, there was a positive correlation between plant palatability and the number of generalist species of chrysomelids (r= 0.420, P<0.05, n=30 tree species), but analogous correlation with specialists was not significant (P>0.1). Hosts with
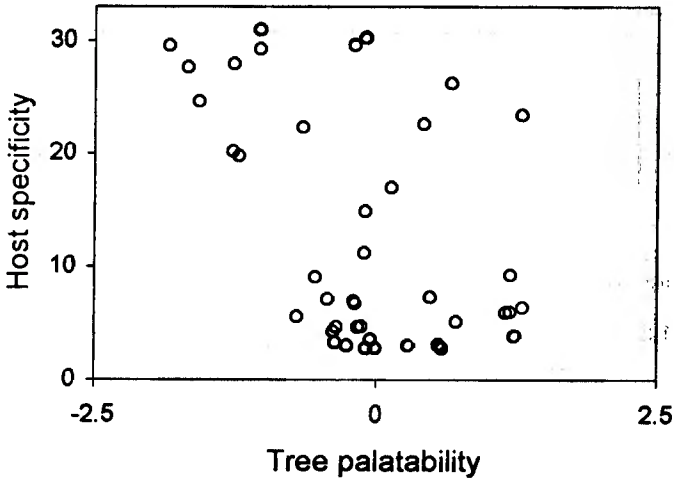
Fig. 7. Relationships between host specificity of chrysomelid species and their distribution optimum with respect to plant palatability.
Each circle represents one chrysomelid species. Tree palatability – species' score on the CCA constrained axis with palatability as the environmental variable (higher scores mean higher palatability); Host specificity - Lloyd's index (higher values mean higher host specialisation).

especially specialised communities (average Lloyd's index > 15) included *Excoecaria, F. microcarpa, Breynia,* and *Homalanthus*; the former three species have low palatability as well.

Plant palatability proved to be a significant explanatory variable for the species composition of chrysomelid communities (the significance of canonical axis P<0.001, Monte Carlo permutation test, 499 permutations, correlation of palatability with this axis r=0.872), but explained only 10% variability in the chrysomelid communities. The scores of chrysomelids on the canonical ("palatability") axis were correlated with their Lloyd's index of host specificity (Spearman r=-0.417, P<0.05; n=42 common species; Fig. 7). In other words, polyphagous species tended to be concentrated especially on palatable hosts.

4. Discussion

The prevalence of Eumolpinae and Galerucinae appeared to be a common feature of arboreal communities in the tropics. For example, chrysomelid communities on 9 of 10 tree species, each from a different family, studied in New Guinea by Basset and Samuelson (1996), were dominated by eumolpines and, similarly as in the present study, galerucines ranked second in terms of species richness. Galerucinae and Eumolpinae were also the most prominent chrysomelid subfamilies in samples from 5 rainforest trees in Borneo (Stork, 1987), while Amazonian rainforest samples were dominated by eumolpines and alticines (Erwin, 1983; Farrell and Erwin, 1988). This taxonomic composition has important ecological consequences, namely the scarcity of larvae in the foliage-feeding chrysomelid communities in the tropics as all species of Eumolpinae and many Galerucinae have subterranean, root-feeding larvae (Jolivet and Hawkeswood, 1995). Predominance of adults in

the foliage-feeding chrysomelid communities may also contribute to their apparently low host specificity, as adults are often more likely to feed on marginal hosts (Jolivet and Hawkeswood, 1995).

Although taxonomy is a very unsatisfactory surrogate of phylogeny, and taxonomic ranks such as genera or families are somewhat arbitrary, there was still a clear difference in patterns of host specificity of chrysomelids when considered within and among plant genera. Within both *Ficus* and *Macaranga*, chrysomelids showed a clear tendency towards oligophagy, feeding often on numerous congeneric hosts. As this pattern was similar in both, mutually independent, cases, as well as in a similar study on weevils feeding on *Piper* spp. (Marquis, 1991), it may be more common. This would have important consequences for the large scale patterns of host specificity in the tropics since species-rich genera are an important part of the tropical vegetation. For instance, three genera (*Macaranga, Glochidion* and *Phyllanthus*) account for 40% of all Euphorbiaceae in New Guinea (van Welzen, 1997), whereas the position of *Ficus* within Moraceae is even more prominent.

The present host specificity estimates are particularly unsatisfactory with regard to the host plant use by widely generalist species. The present study includes only two plant families, while there are a conservative 64 families of woody plants present in one of our study plots (that at Baitabag; L. Balun, pers. comm.). Plant diversity in rain forests is extremely high; for instance, censuses restricted to one hectare and to large trees (DBH>10cm) yielded 97-182 species for a lowland forest in New Guinea (Oatham & Beehler, 1998; Reich, 1998), around 200 species for mid-elevation New Guinean forests (Paijmans, 1970; Wright et al., 1997; Weiblen in press), and a cosmopolitan estimate of between 60 to 150-300 species in the rain forests world-wide (Gentry, 1990; Richards, 1996), belonging often to as many as 50 different families. In comparison with these numbers, the limitations of the present study are obvious.

The similarity of chrysomelid communities does not closely follow the phylogeny (*Ficus*) or taxonomic classification (Euphorbiaceae) of their hosts, although the smaller differences among congeneric hosts and large differences between the families are consistent with the plant taxonomy. It is possible that for congeneric hosts, chrysomelids respond to ambient ecological conditions and quality of various plants, rather than being constrained in their host choice by evolutionarily fixed preferences.

The similarity among chrysomelid communities from different host plant genera was generally low, as they were dominated numerically by specialists and as a consequence of idiosyncratic composition. This is illustrated by a low proportion of variance in their composition, captured by the first two CA axes, and makes the patterns of their similarity difficult to interpret. There were only two notable exceptions to this pattern, where plant genera contained similar chrysomelid communities – the pair *Mallotus* and *Macaranga*, possibly reflecting a close phylogenetic relationship between the two genera, and the pair *Codiaeum* and *Phyllanthus*, which are species from an extreme habitat of rocky river beds. The vegetation in this habitat is often, at least several times a year, submerged after a sudden increase in the water level, following torrential rains. This unpredictable disturbance may explain the low numbers of chrysomelids, as well as a complete absence of specialists, feeding on these plants.

Despite differences between chrysomelid communities on Moraceae and Euphorbiaceae, the number of chrysomelid species able to feed on plants from both families, found in this

study, was relatively large. In contrast, Basset and Samuelson (1996) found 70% of the arboreal chrysomelids able to feed on a single plant family only.

An interesting question is how many rainforest trees are not colonised by chrysomelids. Although all species of *Ficus* had appreciable chrysomelid communities, there were four Euphorbiaceae, each from a different genus, which were practically devoid of chrysomelids. These species represent a heterogeneous group with respect to their habitat, growing in riverine, secondary and primary forest habitats, taxonomy, representing three subfamilies, size, including the smallest and largest Euphorbiaceae studied, as well as palatability. The proportion of unexploited hosts in rainforest vegetation is largely unknown, despite it being an important determinant of the overall species richness and abundance of chrysomelids in the rainforest ecosystems. For example, as reported by Jolivet and Hawkeswood (1995) and confirmed by a current study in the Madang area (Novotny, pers. obs.), Rubiaceae, one of the most species-rich families, has almost no chrysomelids. Basset and Samuelson (1996) found only scarce chrysomelid communities on rainforest trees from several families, with *Ficus* and *Pipturus* (Urticaceae) being the only two hosts, from the ten studied, harbouring species-rich communities.

Farrell and Erwin (1988) suggested that many chrysomelid species in the Amazonian canopy could be host-specific, in comparison with species living in the canopies of temperate forests. As possible causal effect, they cited the higher proportion of tree genera in the tropics that have herbaceous representatives in the temperate zone and the likelihood that these tropical hosts bear some chemical similarity with the chemistry of temperate herbs, often dominated by qualitative defences which could select for host-specific herbivores. This appears to be an open question as their own data do not seem to support the notion of narrow host specificity. They sampled five distinct types of rain forest and found that, on average, chrysomelid species were present in 2.2 (or 44%) from these 5 habitats. This seems to indicate a rather low host specificity, given a probably very low overlap in the species composition of plants sampled in these different forest types.

Polyphagous chrysomelids prefer palatable hosts and palatable hosts are colonised mostly by polyphagous species (note that these are two separate, partly independent patterns). The correlation between plant palatability and host specificity of chrysomelids, reported here, is of interest because the palatability index was derived using a weevil, rather than a chrysomelid, species. Although more extensive screening by various generalist species is necessary in order to establish their validity, such indices might be useful predictors of the community structure of herbivores. There are several theories, suggesting that certain integrated sets of life history traits of plants (life history syndromes) will make them palatable to a wide range of herbivores [for instance, R-strategists (Grime, 1979), growth-dominated plants (Herms and Mattson, 1992), rapidly-growing plants (Price, 1991) and early successional plants (Cates and Orians, 1975)]. Such hypotheses are rarely tested using tropical trees (but see Coley, 1983). The present study indicates that further study of relationships between plant palatability, other life history traits of plants, and the structure of their herbivorous communities may be a promising direction towards better understanding of rainforest insect communities.

Acknowledgements

References

Basset, Y. and Samuelson, G.A. 1996 Ecological characteristics of an arboreal community of Chrysomelidae in Papua New Guinea. In: Jolivet, P. H. A. and Cox, M. L. (eds), Chrysomelidae Biology. Volume 2: Ecological Studies, SPB Academic Publishing, Amsterdam, pp. 243-262.

Berg, C. C. 1989 Classification and distribution of *Ficus*. Experientia 45: 605-611.

Cates, R. G. and Orians, G. H. 1975 Successional status and the palatability of plants to generalized herbivores. Oikos 65: 97-106.

Coley, P. D. 1983 Herbivory and defensive characteristics of tree species in a lowland tropical forest. Ecol. Monogr. 53: 209-233.

Corner, E. J. H. 1965 Check-list of *Ficus* in Asia and Australasia with keys to identification. Gdns' Bull. Straits Settl. 21: 1-186.

Erwin, T. L. 1983 Beetles and other insects of tropical forest canopies at Manaus, Brazil, sampled by insecticidal fogging. In: Sutton, S. L., Whitmore, T. C. and Chadwick, A. C. (eds), Tropical Rain Forest: Ecology and Management, Blackwell Sci. Publ., Oxford, pp. 59-75.

Esser, H.-J., and van Welzen, P. 1997 A phylogenetic classification of the Malesian Hippomaneae (Euphorbiaceae). Syst. Bot. 22: 617-628.

Farrell, B. D. and Erwin, T. L. 1988 Leaf-beetle community structure in an amazonian rainforest canopy. In: Jolivet, P., Petitpierre, E. and Hsiao, T. H. (eds), Biology of Chrysomelidae, Kluwer Academic Publishers, Dordrecht, pp. 73-90.

Flowers, R. W. and Janzen, D. H. 1997 Feeding records of Costa Rican leaf beetles (Coleoptera: Chrysomelidae). Fla. Ent. 80: 334-366.

Gentry, A.H. (ed) 1990 *Four Neotropical Forests*. Yale University Press, New Haven.

Gressitt, J. L. 1959 Host relations and distribution of New Guinea Hispine beetles. Proc. Hawaii. ent. Soc. 17: 70-75.

Grime, J. P. 1979 Plant strategies and vegetation processes. Wiley, Chichester.

Herms, D. A. and Mattson, W. J. 1992 The dilemma of plants: to grow or defend. Q. Rev. Biol. 6: 283-335.

Heywood, V. H. (ed) 1993 Flowering Plants of the World. B. T. Batsford Ltd, London.

Höft, R. 1992. Plants of New Guinea and the Solomon Islands. Dictionary of the Genera and Families of Flowering Plants and Ferns. Wau Ecology Institute (Handbook No. 13), Wau.

Jolivet, P. and Petitpierre, E. 1976 Les plantes-hôtes connues des *Chrysolina* (Col. Chrysomelidae) : essai sur les types de selection trophique. Annls Soc. ent. Fr. 12: 123-149.

Jolivet, P. 1989 Sélection trophique chez les Hispinae (Coleoptera Chrysomelidae Cryptosoma). Bull. mens. Soc. linn. Lyon 58: 297-317.

Jolivet, P. and Hawkeswood, T. J. 1995 Host-plants of Chrysomelidae of the World. An Essay about the Relationships between the Leaf-beetles and their Food-plants. Backhuys Publishers, Leiden.

Lawton, J. H. and Schröder, D. 1977 Effects of plant type, size of geographical range and taxonomic isolation on number of insect species associated with British plants. Nature 265: 137-140.

Lepš, J. 1993 Taylor's power law and measuring variation in the size of populations in space and time. Oikos 68: 349-356.

Lloyd, M. 1967. Mean crowding. J. anim. Ecol. 36: 1-30.

Marquis, R. J. 1991. Herbivore fauna of *Piper* (Piperaceae) in a Costa Rican wet forest: diversity, specificity and impact. In: Price, P. W., Lewinsohn, T. M., Fernandes, G. W., Benson, W. W. (eds.) Plant - Animal Interactions: Evolutionary Ecology in Tropical and Temperate Regions. London, John Wiley & Sons, pp 179-208.

McAlpine, J. R., Keig, G., Falls, R. 1983 Climate of Papua New Guinea. CSIRO and Australian National University Press, Canberra

Oatham, M. and Beehler, B. M. 1998 Richness, taxonomic composition and species patchiness in three lowland forest tree plots in Papua New Guinea. In Dallmeier, F. and Comiskey, J. A. (eds.) Forest biodiversity research, monitoring and modelling: Conceptual background and Old World case studies. UNESCO and Parthenon Publishing Group, Paris and New York, pp 613-631.

Ohmart, C. P. 1996 Population dynamics of chrysomelid beetles feeding on *Eucalyptus*. In: Jolivet, P. H. A. and Cox, M. L. (eds), Chrysomelidae Biology. Volume 2: Ecological Studies, SPB Academic Publishing, Amsterdam, pp 263-269.

Paijmans, K. 1970. Analysis of four tropical rain forests in Papua New Guinea. J. trop. Ecol. 58: 77-101

Price, P. W. 1991 The plant vigor hypothesis and herbivore attack. Oikos 62: 244-251.

Rank, N., Smiley, J. and Koepf, A. 1996 Natural enemies and host plant relationships for Chrysomeline leaf beetles feeding on Salicaceae. In: Jolivet, P. H. A. and Cox, M. L. (eds), Chrysomelidae Biology. Volume 2: Ecological Studies, SPB Academic Publishing, Amsterdam, pp 147-171.

Reich, J. A. 1998. Vegetation. Part 1: A comparison of 2 two-hectare tree plots in the Lakekamu basin. In: Mack, A. (ed.), A Biological Assessment of the Lakekamu Basin, PNG. Conservation International, Washington, pp 25-35.

Richards, P. W. 1996 The Tropical Rain Forest. Cambridge University Press, Cambridge.

Stork, N. E. 1987 Arthropod faunal similarity of Bornean rain forest trees. Ecol. Ent. 12:219-226.

Strong, D. R. J. 1977 Rolled-leaf hispine beetles (Chrysomelidae) and their Zingiberales host plants in middle America. Biotropica 9: 156-169.

Tahvanainen, J. 1983 The relationship between flea beetles and their cruciferous host plants: the role of plant and habitat characteristics. Oikos 40: 433-437.

van Welzen, P. C. 1997 A preliminary checklist of Euphorbiaceae of Thailand and the Malesian area. Malesian Euphorbiaceae Newsletter 6: 1-31.

Webster, G. L. 1975 Conspectus of a new classification of the Euphorbiaceae. Taxon 24: 593-601.

Weiblen, G. in press. Forest composition and structure of a one hectare plot in the Crater Mountain Wildlife Management Area, Papua New Guinea. Science in New Guinea.

Whitmore, T. C. 1979 Studies in *Macaranga*, X. – potentially commercial species in new Guinea. Commonw. For. Rev. 58: 271-272.

Whitmore, T. C. 1980 *Macaranga*. In: Airy Shaw, H. K., The Euphorbiaceae of New Guinea, Kew Bulletin Additional Series 8, Royal Botanic Gardens, Kew, pp. 123-162.

Wright, D. D., Jessen, J. H., Burke, P. and Garza, H.G.D.S. 1997 Tree and liana enumeration and diversity on a one-hectare plot in Papua New Guinea. Biotropica 29, 250-260.

Appendix 1. Chrysomelids feeding on the studied trees.

Morphospecies code is followed by name (if known), host specificity category (G – generalist, S – specialist, r – too rare to decide), the number of individuals, the number of hosts, and, for specialists, the principal host plant genus.

Alticinae:
CHRY070 (r, 1, 1); CHRY068 – *Nisotra* sp. (G, 84, 5); CHRY069 – *Sutrea* sp. (r, 1, 1); CHRY058 – *Xenidea* sp. (r, 9, 2); CHRY096 (r, 2, 1).

Criocerinae:
CHRY053 – *Lema connectens* Baly (r, 1, 1); CHRY093 – *Lema staudingeri* Jacoby (r, 14, 4)

Cryptocephalinae:
CHRY085 – *Cadmus multinodosus* (Gressitt) (r, 5, 2); CHRY043 – *Coenobius* sp. (S, 21, 1, *Ficus*); CHRY099 – *Melatia ?glochidionis* (Gressitt) (S, 39, 1, *Homalanthus*); CHRY090 – *Melatia* sp. (r, 3, 2).

Eumolpinae:
CHRY072 – *Cleorina* sp. (S, 228, 7, *Macaranga*); CHRY061 – *Deretrichia* sp. (r, 7, 5); CHRY076 – *Deretrichia* sp. (S, 17, 5, *Macaranga*); CHRY054 – *Deretrichia* sp. (S, 261, 12, *Homalanthus*); CHRY023 – *Deretrichia* sp. (r, 14, 9); CHRY108 – *Deretrichia* sp. (G, 18, 6); CHRY124 – *Deretrichia* sp. (r, 7, 3); CHRY027 – *Rhyparida* sp. (G, 106, 8); CHRY025 – *Rhyparida basalis* Baly (G, 148, 5); CHRY064 – *Rhyparida* nr. *basalis* Gressitt (r, 1, 1); CHRY031 – *Rhyparida cacaovora* Gressitt (G, 180, 24); CHRY019 – *Rhyparida calami* Gressitt (G, 52, 14); CHRY001 – *Rhyparida coriacea* Jacoby (G, 1041, 27); CHRY042 – *Rhyparida dejecta* Gressitt (r, 2, 2); CHRY024 – *Rhyparida duni* Gressitt (S, 106, 3, *Ficus*); CHRY052 – *Rhyparida fasciata* Baly (G, 41, 10); CHRY021 – *Rhyparida fruhstorferi* Jacoby (G, 50, 13); CHRY063 – *Rhyparida fulvicornis* Jacoby (r, 3, 3); CHRY046 – *Rhyparida huona* Gressitt (G, 634, 17); CHRY026 – *Rhyparida* nr. *impressipennis* Bryant (G, 25, 11); CHRY079 – *Rhyparida lineolata* Gressitt (S, 26, 6, *Macaranga*); CHRY018 – *Rhyparida ?normalis* (r, 5, 4); CHRY014 – *Rhyparida picticollis* Gressitt (G, 123, 19); CHRY084 – *Rhyparida pruinicollis* Gressitt (G, 68, 10); CHRY037 – *Rhyparida sinuata* Gressitt (G, 133, 16); CHRY078 – *Rhyparida* sp. (S, 673, 1, *Excoecaria*); CHRY113 – *Rhyparida* sp. (S, 19, 3, *Macaranga*); CHRY071 – *Rhyparidella casuarinae* Gressitt (r, 4, 3); CHRY082 – *Rhyparidella sewana* Gressitt group (G, 70, 7); CHRY002 – *Rhyparidella sobrina* (Bryant) group (S, 1803, 20, *Ficus*); CHRY032 – *Rhyparidella* sp. (r, 10, 3); CHRY012 – *Rhyparidella* sp. (r, 6, 5); CHRY022 – *Rhyparidella* sp. (r, 4, 3); CHRY044 – *Rhyparidella* sp. (r, 4, 2); CHRY006 – *Rhyparidella* sp. (r, 1, 1); CHRY028 – *Rhyparidella* sp. (r, 1, 1); CHRY013 – *Stethotes* nr *integra* Jacoby (r, 1, 1); CHRY030 – *Stethotes lateralis* Baly (G, 879, 19); CHRY017 – *Stethotes* nr *nigritula* Jacoby (r, 4, 3); CHRY056 – *Thyrasia?* sp. (G, 82, 14); CHRY050 (r, 4, 4); CHRY029 (S, 118, 5, *Macaranga*); CHRY098 (r, 1, 1); CHRY104 (r, 2, 2); CHRY119 (r, 1, 1).

Galerucinae:

CHRY004 – *Atysa* sp. (S, 125, 6, *Ficus*); CHRY051 – *Atysa* sp. (S, 31, 2, *Ficus*); CHRY059 – *Atysa* sp. (r, 3, 3); CHRY040 – *Aulacophora* sp. (r, 8, 5); CHRY066 – *Aulacophora* sp. (r, 2, 1); CHRY067 – *Aulacophora* sp. (r, 2, 1); CHRY110 – *Aulacophora* sp. (r, 2, 1); CHRY073 – *Aulacophora* sp. (r, 1, 1); CHRY127 – *Aulacophora* sp. (r, 1, 1); CHRY007 – *Aulacophora* sp. (G, 17, 4); CHRY041 – *Aulacophora* sp. (G, 106, 7); CHRY055 – *Aulacophora* sp. (G, 33, 6); CHRY091 – *Cassena* sp. (r, 7, 4); CHRY097 – *Cassena* sp. (r, 1, 1); CHRY016 – *Lomirana* sp. (G, 138, 12); CHRY047 – ?*Monolepta* sp. (r, 1, 1); CHRY074 – ?*Monolepta* sp. (r, 1, 1); CHRY003 – *Sastra* sp. (S, 316, 4, *Ficus*); CHRY039 – *Sastra* sp. (S, 21, 7, *Ficus*); CHRY033 – *Sastra* sp. (r, 13, 7); CHRY038 – *Sastra* sp. (r, 7, 5); CHRY057 – *Sastra* sp. (r, 4, 2) CHRY081 (S, 748, 1, *Excoecaria*); CHRY009 (S, 163, 12, *Ficus*); CHRY020 (S, 85, 9, *Ficus*); CHRY060 (r, 1, 1); CHRY075 (r, 1, 1); CHRY083 (r, 1, 1); CHRY087 (S, 17, 1, *Excoecaria*); CHRY088 (S, 27, 2, *Breynia*); CHRY089 (G, 129, 3); CHRY105 (r, 1, 1); CHRY111 (r, 2, 1); CHRY117 (r, 1, 1); CHRY120 (r, 5, 2); CHRY122 (r, 1, 1); CHRY123 (r, 1, 1).