

Host specificity of arboreal and free-living insect herbivores in rain forests

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Available information about the host specificity of arboreal and free-living insect herbivores in rain forests is scarce, but suggests that polyphagy may be more widespread than previously thought. The study of the arthropod fauna associated with an overstorey tree in Australia, *Argyrodendron actinophyllum* (Sterculiaceae), supports this contention. A conservative 11% of herbivore species foraging within this tree appear to be specialists, whereas this proportion decreases further to 3.0–4.5% when non-herbivore species are included. *Argyrodendron actinophyllum* presents several features which may promote a polyphagous strategy among herbivores. These observations are discussed in the wider context of ecological and evolutionary pressures shaping feeding strategies of insect herbivores in rain forests. These selection pressures include principally plant biochemistry, predation pressure of generalist predators, and structural diversity and environmental unpredictability of rainforest environments. The strength of association between herbivores and rainforest host-trees is likely to depend on three factors, acting at both the tree and rainforest community level: chemical traits of foliage (including chemical defences and nutrient levels), young foliage availability and enemy-free space. Given the complex interactions possible among these factors, rainforest host-trees may sustain herbivore faunas ranging from highly specialized to highly generalist.

KEY WORDS:—Arboreal arthropods – *Argyrodendron actinophyllum* – enemy-free space – insect-plant interactions – host specificity – nutrient availability – plant apparency – species richness – rain forests.

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INTRODUCTION

The species richness of arthropods, like that of many other animals, is higher in tropical habitats than in temperate habitats, and this is particularly well-documented in the canopy of tropical rain forests (Erwin, 1988). Four categories

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of hypotheses, which are further detailed in Pianka (1966) and in Turner, Gatehouse & Corey (1987), have been developed to account for this situation: (1) historic hypotheses postulating a greater stability of the tropical climate, since the fauna of temperate lands has been depleted by recent glaciation; (2) structural hypotheses, in which tropical ecosystems are regarded as providing more ecological niches than temperate ecosystems; (3) dynamic hypotheses, where predation and competition in the tropics are thought to be set to levels allowing higher speciation rates and; (4) energetic hypotheses, in which it was originally stated that higher biological stability in the tropics permits higher species specialization. This last concept was improved and redefined as the control of solar energy over organic diversity in conditions of non-limited water resources (further detailed in Turner *et al.*, 1987). The application of the second tenet led Erwin (1982), who sampled the beetle fauna of the rainforest tree *Luehea seemannii* (Tiliaceae) in Panama with canopy fogging, to report that 20% of the insect herbivore species obtained were host-specific to this tree and to suggest that there are perhaps as many as 30 million tropical arthropod species, instead of the conservative 1.5 million species usually accepted. Stork (1988) reanalysed the data provided by Erwin and estimated a range of 10 to 80 million arthropod species. However, similar discussion of species richness with an emphasis on other insects (Hemiptera) by Hodkinson & Casson (1991) yielded considerably lower estimates of total arthropod species (1.8 to 2.6 million species).

In temperate woodlands, many arboreal insect herbivores show a high degree of host specificity (e.g. reviews in Crawley, 1983; Strong, Lawton & Southwood, 1984). In these forests, monophagy is particularly advantageous since food-plants usually grow in large, often monospecific patches and, therefore, the costs of search for herbivores are negligible (Crawley, 1983). However, insect communities in temperate forests are neither organized into 'discrete' communities (i.e. saturation with host-specific insects) nor into a 'continuum' of species (i.e. saturated with generalists), but their organization fits somewhere between these two extremes (Futuyma & Gould, 1979).

Conversely, the host specificity of tropical insects, and particularly that of arboreal herbivores, is not well documented despite being a subject of controversy. Nevertheless, available information indicates that certain tropical insects, which are concealed feeders (e.g. Bruchidae and other seed-eaters: review in Janzen, 1981; leaf-mining Hispinae: Jolivet, 1988) or mainly restricted to herbaceous plants and vines (e.g. Ithomiinae, Satyrinae and Heliconiinae on Solanaceae, Graminae and Passifloraceae, respectively, all reviewed in Gilbert & Smiley, 1978; some Chrysomelidae: Jolivet, 1988), appear to be rather host-specific. Selection pressures exerted upon these herbivores may differ from those acting upon arboreal and free-living phytophagous insects, which presumably represent the majority of rainforest herbivores (free-living herbivores include folivorous chewers and sap-suckers which exploit freely the surface of leaves, unlike miners, gall-makers, shoot-borers and seed-eaters). Concealed feeders present a high physical 'intimacy' with their host, and therefore their high host specificity is not so unexpected (Mattson *et al.*, 1988), although the ecological and evolutionary reasons for their concealment are extremely interesting. For example, Janzen (1981) investigated invertebrate seed predators in a Costa Rican forest and reported bruchid beetles and mining moths as being quite

specialized, whereas sap-feeding bugs feeding externally were quite polyphagous. Further, selection pressures exerted on phytophagous insects may contrast according to association with either woody or herbaceous plants, for two main reasons. Firstly, different plant architectures may affect both host-plant apparency to herbivores and herbivore apparency to predators and parasitoids diversely (Strong *et al.*, 1984). Unapparent plants, such as herbs, usually interact with fewer species than apparent plants, such as trees, and these species usually consist mostly of specialists (stepwise coevolution: Fox, 1981). In part, this argument may explain why close correspondence between faunal similarity and taxonomic affinity of host-plants (related to chemical similarity) have been found in the case of herbaceous plants (e.g. Berenbaum, 1981), but not in the case of woody plants (e.g. Futuyma & Gould, 1979; Holloway & Hebert, 1979). Secondly, and possibly as a corollary (Fox, 1981; but see converse opinion in Coley, 1983), herbs and vines rely more on qualitative defences (toxins, such as alkaloids, saponins, cardiac and cyanogenic glycosides, glucosinolates etc.) than trees, which are better protected by quantitative, dose-dependent defences (digestibility reducers, such as tannins, other polyphenols, silica and fibre) (Feeny, 1976; Futuyma, 1976; Waterman & McKey, 1989). For example, Rowell (1978, 1985) documented the narrow host specificity of rainforest acridids feeding on plants located in the field layer and attributed this strategy to the high diversity of plant chemicals. In that example, most food-plants were herbaceous, well-protected and nutrient-rich (Rowell, 1985). Hence, there is a need to distinguish between concealed and external feeders, and between woody and herbaceous hosts, when discussing insect host specificity in rain forests. The present paper explores the host specificity of arboreal and free-living insect herbivores more specifically.

The arboreal arthropod fauna of the Australian rainforest tree *Argyrodendron actinophyllum* has been subjected to detailed investigation from several perspectives, including taxonomic composition, guild structure and species diversity of the arthropod community; temporal and spatial distribution of associated arthropods; relations between host phenology and herbivores, grazing damage etc. (Basset, 1988–1990, 1991 a–d; Basset & Kitching, 1991). Overall, this represents one of the most comprehensive sampling studies yet attempted of a single-host rainforest canopy fauna and it provided an opportunity to document and to discuss the host specificity of insects associated with this tree species. The present paper is organized as follows: after briefly reviewing existent information about the host specificity of arboreal insect herbivores in rain forests, that of phytophagous insects associated with *A. actinophyllum* is detailed. Then, respective selection pressures shaping monophagy and polyphagy among free-living arboreal herbivores in rain forests are discussed with particular reference to the new body of data. The discussion concludes with a tentative conspectus on this issue.

In order to avoid ambiguity, several terms require clarification. In the text, 'herbivores' do not include wood-eaters (i.e. xylophagous and xylomycetophagous species), which are often associated with dead or decaying vegetation, but only phyllophages. Host specificity may be discussed either entomocentrically (i.e. relating to the proportion of host-specific insects within a particular taxa), or phytocentrically (i.e. relating to the proportion of host-specific insects feeding upon a particular host-plant). Often, the latter will be

emphasized in this paper. Furthermore, insect-host specificity may differ between juvenile and adult stages, and the present discussion concerns the latter category of insects primarily. Lastly, 'monophagous' refers to species restricted to host species belonging to the same family, 'oligophagous' to species restricted to a few hosts from related families or to very few hosts from unrelated families, and 'polyphagous' to species feeding upon a large array of hosts from different families. Specialist and generalist feeders refer to monophagous plus oligophagous species, and to polyphagous species, respectively.

HOST SPECIFICITY OF ARBOREAL HERBIVORES IN RAIN FORESTS: A BRIEF REVIEW

A substantial proportion of information about insect host-specificity in rain forests has been collected from the field layer. The host specificity of arboreal rainforest herbivores is still poorly known. Some non-herbivore insects, which are regularly associated with arboreal habitats, appear to be less host-specific in the tropics, and particularly in rain forests, than in temperate conditions (e.g. Scolytidae: Beaver, 1979; Ichneumonidae: Gauld, 1986). The host specificity of tropical parasitoids has been debated intensely, but a distinctive feature of rainforest parasitoid faunas appears to be the high proportion of egg parasitoids (i.e. Scelionidae, Mymaridae and Trichogrammatidae) which may be generalists, but not always (see review in Noyes, 1989). Literature surveys of particular arboreal arthropod groups suggest that a high proportion of their species may not be restricted to certain host-trees: parasitoids attacking gall-makers (Askew, 1980), arboreal predators (Jermy, 1988), fungal-feeders (Kukor & Martin, 1987) and wood-eaters (Hamilton, 1978). However, no hard data exist on the occurrence of polyphagy within these groups in rain forests, although Atkinson & Equihua (1986) showed that polyphagous species of wood-eaters are more common in tropical areas exposed to high rainfall, since humid climates enhance xylomycetophagous habits.

With reference to rainforest herbivores, an interesting data set was provided by insecticidal fogging of the arboreal fauna associated with the tree *Luehea seemannii* in Panama, with particular reference to Hemiptera and Coleoptera (Erwin & Scott, 1980; Erwin, 1982). Wolda (1979), studying the former group, stressed that leaf production on vines may exert a greater influence on local species richness than the leaf production of *Luehea* itself. Seventy percent of the homopteran species collected from *Luehea* were known to occur on Barro Colorado Island (Wolda, 1979). Erwin (1982) discussed beetle specificity on *Luehea* and suggested that 20%, 5%, 10% and 5%, respectively, of herbivores, predators, fungivores and scavengers were host-specific to this tree. These estimations were based on subjective impression alone. There is no intention here to discuss arthropod species richness in rain forests, as did Erwin (1982) and Stork (1988). However, two important comments are necessary about the extrapolations made by the former author regarding insect host specificity on *Luehea*: Firstly, Erwin included wood-eaters in the herbivore category and, therefore, implied that 20% of wood-eating species are host-specific to *Luehea*, an unrealistically high proportion. This point is of vital importance, since, on *Luehea* as on *Argyrodendron* (see next section), a substantial proportion of beetle species is represented by wood-eaters, such as most Curculionoidea and Cerambycidae. Secondly, the fogging programme of Erwin & Scott (1980) was performed

during the day, as three discrete sampling events, on 19 trees. The lack of replicates in time (both on a seasonal basis and on a diurnal basis) may have prevented the accurate assessment of host specificity, since rare species may appear to be more specialized than they really are (Redfearn & Pimm, 1988), and discrete sampling usually reveals a higher proportion of 'rare' species than continuous sampling (Basset & Kitching, 1991).

Janzen & Waterman (1984) investigated the host specificity of sphingiid and saturniid moths from herbaceous and woody host-plants in Costa Rica. They found that, whilst the former is rather specialized, the latter is less host-specific. Further, Janzen (1988) studied the caterpillar fauna of a dry forest in Costa Rica and estimated that over 50% of the species were monophagous and that polyphagous species represented only a small proportion of the fauna. However, only 37% of species surveyed were external feeders. Stork (1987) compared the arboreal fauna of several Bornean trees fogged with insecticide and concluded that taxonomic relatedness of trees was not an important factor of faunal similarity for certain phytophagous groups, such as Galerucinae, Homoptera and Heteroptera. He interpreted this to mean that these groups are not highly host-specific. Couturier, Lachasie & Tsacas (1985: table 6) reported a high proportion of polyphagous species in plant-breeding drosophilids of West African rain forests (monophagous species: 15.4%; oligophagous species: 32.7%; polyphagous species: 51.9%). Furthermore, within highly specialized herbivore groups as Aphidoidea, the proportion of polyphagous species appears higher in the tropics than in temperate forests (Dixon *et al.*, 1987).

In summary, although the narrow host-specificity of certain rainforest insects cannot be denied, there is small, but growing evidence that the occurrence of polyphagy among rainforest arthropods, including that among insect herbivores, may be more widespread than previously thought. However, the extent to which herbivores rely on this feeding strategy varies among insect groups and it may also vary with the characteristics of the rain forests and of the host-trees studied.

HOST SPECIFICITY OF INSECTS ASSOCIATED WITH *ARGYRODENDRON ACTINOPHYLLUM*

Argrodendron actinophyllum (Bailey) Edlin, 1935 ('black booyong') is a tall Sterculiaceae, reaching up to 50 m high. The phenology and distribution of this evergreen tree are outlined in Boland *et al.* (1984) and in Basset (1989). Surveys of arthropods associated with *A. actinophyllum* were conducted in a stand of complex notophyll vine forest (warm subtropical rain forest), in the Mount Glorious State Forest (27°19'20"S, 152°44'55"E, altitude 700 m), some 30 km NW of Brisbane, Queensland, Australia.

Arthropod sampling was performed by two main techniques. Firstly, five composite interception traps, consisting of malaise and window trap sub-units, were sited in the crowns of five mature black booyong trees, free of vines. Arthropods were collected continuously, day and night, with these traps, which were surveyed weekly during 1986 and 1987. Secondly, 240 samples of 0.7 m² of leaf area were fogged with CO₂ from ten trees ('restricted canopy fogging'). Both sampling procedures were detailed and discussed elsewhere (Basset, 1988–1990). Specimens were sorted to families and morphospecies and subsequently examined by specialist taxonomists (Basset, 1991a). However, most of

Hymenoptera, Parasitica, Diptera and imagines of Lepidoptera were sorted to family only.

Since sampling was restricted to one particular host-tree species, little can be stated directly about the host specificity of insect herbivores and wood-eaters associated with this tree. Instead, host specificity was deduced from the following cross-observations, which are detailed for each species in Basset (1989): (a) various feeding trials for chewing species with the foliage of *A. actinophyllum*, other rainforest hosts and *Eucalyptus* spp. (in which live insect specimens were obtained by hand-collecting, beating or using modified interception traps for catching specimens alive); (b) communication from various taxonomists who identified the material and searched the relevant literature (although this was difficult due to the general lack of knowledge about the identity and the biology of most Australian rainforest insects); (c) observation during many hours spent by the author in the canopy; (d) qualitative comparison between herbivore species collected in black booyong crowns and those collected with a control interception trap in the field layer (herbivores foraging within several layers of rain forest are more likely to be generalists, but not obligatory so); and (e) rearing of wood-borers from dead branches of *A. actinophyllum* and of other rainforest trees.

More than 50 000 arthropods were collected from the crowns of *A. actinophyllum* during the three-year field study. Herbivores and wood-eaters were extensively sorted from this material and included 124 species of wood-eaters, 93 sap-suckers, 58 chewers, four gall-makers, three miners and one shoot-borer. A herbivore checklist is detailed in Basset (1989), and is also available from the author on request. Comparison of this list with similar Australian records for *Acacia* spp. (e.g. Froggatt, 1923; Van den Berg, 1980; New, 1984) and *Eucalyptus* spp. (e.g. Froggatt, 1923; Morrow, 1977; Carne & Taylor, 1978; Ohmart, Stewart & Thomas, 1983) revealed very few similarities at the generic level and none of them at the species level. Although Froggatt (1923) cited examples of forest pests associated with several rainforest hosts, such as *Toona australis*, *Ficus macrophylla* and *Araucaria* spp., the only published and relatively exhaustive list of herbivores associated with Australian rainforest trees is found in Lowman (1985). In her study, several genera were common to *Nothofagus moorei* and *A. actinophyllum*, but most specimens were not identified to species. Therefore, judging from crude faunal lists, the herbivore fauna associated with *A. actinophyllum* appears to be quite distinct from those associated with other Australian host-trees, although this point remains to be clarified regarding other rainforest trees.

Most of the common insect herbivores collected either by interception traps or fogging have been observed to feed upon *A. actinophyllum* in the field or in captivity (detailed in Basset, 1989). However, a substantial proportion of herbivore species, represented by few individuals in the collections and whose feeding records could not be verified, may have been collected incidentally. All gall-makers, miners and shoot-borers are expected to be monophagous, or possible oligophagous. Other candidates for a specialized diet include two Psylloidea, one Phlaeothripidae and three Curculionidae, whose nymphs and larvae feed on young foliage. All these species are yet undescribed and are known from black booyong foliage only (K. L. Taylor, E. C. Zimmerman and J. Palmer, personal communication). *Argyrodendron actinophyllum* flowers are small,

inconspicuous and do not attract many pollinators, except bees (Basset, 1989). The flowers are damaged by the two above psyllid species, one unidentified species of Lepidoptera, one of Cecidomyiidae and one of Ceratopogonidae. All these species may be specialists. It is probable that other such specialized species await recognition among the Anthomyiidae, Chloropidae, Lygaeidae, Miridae, Cicadellidae, Lepidoptera and Thysanoptera.

Some Geometridae collected from the foliage of *A. actinophyllum* fed upon both young eucalypt foliage and young leaves of the study tree. Some Lymantriidae were observed to feed *in situ* both on black booyong foliage and on orchid floral buds. The Coccoidea recorded appear to be widespread pests (P. J. Gullan, personal communication). No larvae of Chrysomelidae were collected from the foliage of *A. actinophyllum*. The adults most commonly encountered and which feed on this species belong to the subfamilies Eumolpinae and Alticinae. The larvae of the former are notorious as polyphagous root-feeders, whereas only part of the latter share this diet (Jolivet, 1988). A substantial proportion of adult Eumolpinae are known to be polyphagous and some are pests of tropical crops (Jolivet, 1987), such as certain genera which were represented by several species on *A. actinophyllum*. Furthermore, some chrysomelids collected in the present study were also recorded from *Nothofagus moorei* (C. A. M. Reid, personal communication). Others, obtained by fogging and feeding upon *A. actinophyllum*, were collected in the control interception trap set up in the field layer. Also this applied to some Cicadellidae. Most of the Drosophilidae recorded are associated with fungi or rotting material (I. R. Bock, personal communication). A substantial proportion of Cerambycidae, reared from *A. actinophyllum* branches, appears to be polyphagous, after consultation of checklists such as those provided by Williams (1985) and Webb, Williams & de Keyzer (1988). It is probable that this applies to other wood-borers, such as Curculionoidea and Buprestidae. Nearly all Scolytidae collected are xylomycetophagous and, therefore, polyphagous in their utilization of host-trees (R. A. Beaver, personal communication; and see Beaver, 1979). No insects were recorded from *A. actinophyllum* seeds, but the study was carried out during years of low seed yield and few seeds could be inspected *in situ* for insect damage. A number of Chloropidae, Drosophilidae and Muscidae were reared from fallen and rotten seeds, but these species are unlikely to be specialists.

A further argument towards the low host-specificity of most herbivores feeding upon *A. actinophyllum* pertains to the distribution of herbivore seasonal ranges. In light of several considerations detailed in later sections, one can reasonably expect that the occurrence of most specialized feeders associated with *A. actinophyllum* is likely to be restricted to temporal windows of young foliage presence. Out of a total of 70 species which could be investigated in this regard, only 17 (24%) show a seasonal range shorter than 21 weeks, the average length of the leaf-flushing season for *A. actinophyllum* (Basset, 1989, 1991b). Although this observation does not establish that these species are specialists, it is most probable that the other 53 (76%) species are polyphagous.

Overall, field sampling suggests that specialized species are not numerous on *A. actinophyllum*. It is possible that the sampling of more active insects with interception traps, may result in a bias toward mobile polyphagous species, but sampling of foliage insects by restricted canopy fogging indicated a similar low proportion of specialist feeders. A conservative 11% of herbivore species foraging

within *A. actinophyllum* crowns (17 species out of 156 recognized) are considered to be mono- or oligo-phagous. Probably, there are few arboreal arthropods, of non-herbivore trophic habits, which are restricted to this tree. The unsorted non-herbivore material, the possible sibling species and the non-herbivore 'specialists' might increase this specialist load to, say, 30–40 species. This estimation represents about 3.0 to 4.5% of all the species recognized from both trap and fogging collections (about 900 species in total). In particular, the proportion of host-specific beetle species obtained from *A. actinophyllum* with fogging amounted to less than 5%. This figure is much lower than the estimated 13.5% of host-specific beetles which were fogged from *Luehea* trees (Erwin, 1982). Similar information from temperature host-trees suggests that on average at least 20% of species constituting assemblages of arboreal herbivores are specialists, but this figure varies greatly among hosts (e.g. Futuyma & Gould, 1979; Covassi & Masutti, 1980; Claridge & Wilson, 1981; Neuvonen & Niemela, 1981).

SELECTION PRESSURES SHAPING MONOPHAGY IN RAIN FORESTS

Selection pressures leading rainforest herbivores to adopt monophagy or polyphagy may include two main types of ecological and evolutionary constraints: those derived from the component community (*sensu* Root, 1973; the host-tree and its associated fauna), and those derived from the compound community (the rain forest). To discuss the extent to which component communities exist individually in rain forests is beyond the scope of this paper, but this concept is certainly convenient and helpful in order to discuss the organization of phytophagous insect communities (for example, see the contrast between the ideas of 'diffuse coevolution' and 'step-wise coevolution' in Fox, 1981). Primarily, the first type of constraints are functions of host characteristics, which include chemical defences, nutrient levels, host abundance and phenology, while the second type derive from the chemical and structural diversity of the plant community (and its concomitant influence on the availability of food resource and insect dispersal), enemy-free space and mesoclimatic factors.

The view that the vast array of chemical defences displayed by rainforest plants should select for a narrow diet among insect herbivores is well established, particularly because costs of specializing (i.e. those related to host location and selection, and herbivore dispersal) may be outweighed by improved physiological performance and concomitant increased insect fitness (e.g. Ehrlich & Raven, 1964; Janzen, 1985, 1988; Waterman & McKey, 1989). In particular, plant chemical defences are expected to be well-developed when interspecific competition is high (Burdon & Chilvers, 1974), such as in rainforest environments. However, one of the underlying assumptions of the physiological efficiency hypothesis (that the efficiency and competitive ability of specialists is higher than that of generalists) has been challenged on repeated occasions (e.g. Smiley, 1978; Fox & Morrow, 1981). This hypothesis is implicit in the general scheme of coevolution proposed by Ehrlich & Raven (1964), which further implied that high species diversity in rain forests is a result of herbivore pressure interacting with plant chemical defences. However, there are indications that coevolved insect-plant systems, such as those hypothesized by Ehrlich & Raven (1964) are rather rare in natural ecosystems, and particularly on woody hosts,

where the potential for interaction between plant and numerous herbivores is high (Fox, 1981: diffuse coevolution; Craig *et al.*, 1988). Several pieces of empirical evidence support this argument, including the lack of correspondence between the species-rich Dipterocarpaceae in lowland rain forests of south-east Asia and the paucity of associated lepidopteran herbivores (Holloway, 1989), and the lack of influence of tree-feeding Papilionidae on the phytochemistry of their hosts (Scriber, 1988).

Undoubtedly, the interpretation of insect-plant interactions mediated by chemical defences progressed with the formulation of the defence theory and the plant apparency concept (Feeny, 1976; Rhoades & Cates, 1976; Futuyma, 1976; Fox, 1981), which predicts that the breadth of a herbivore's diet depends upon the apparency and mode of defence of its food-plant: herbivores using unapparent plants defended by toxins should tend to be more specialized than those restricted to plants relying on digestibility-reducers. However, there are several problems involved with this hypothesis, such as the difficulty of characterizing qualitative and quantitative defences, and it needs certainly some refinement (Fox, 1981; Barbosa, 1988). Further, Coley (1983) suggested, on the basis of her examination of plant grazing rates in a Costa Rican rain forest, that pioneer and persistent hosts are equally easy for herbivores to discover. The general validity of this observation remains to be tested formally, since leaf damage, which is usually highly influenced by a few lepidopteran species, may be, in some instances, a poor indicator of the preferences exhibited by the whole herbivore community (Basset, 1991c).

Coley, Bryant & Chapin (1985) elaborated the theory of resource availability, which states basically that resource limitation selects for slow plant growth rates which, in turn, favour large investment in defence. Their hypothesis clearly explains differences in herbivore pressure on plants differing in their successional status (pioneer/climax species: Coley, 1983) and in their general growth strategy (evergreen/deciduous species: MacLean & Jensen, 1985). Lastly, adding to the importance of chemical defences in herbivore diet specialization, it has been argued that the existence of host-induced chemical defences may maintain a selection pressure for sympatric speciation of herbivores (e.g. Edwards & Wratten, 1983). However, there is evidence to suggest that evergreen trees and, therefore, a high proportion of rainforest trees, may have a limited capacity of long-term induced response to defoliation, in comparison with deciduous trees (Tuomi *et al.*, 1988).

Therefore, it appears difficult to deny the importance of chemical defences, both at component and compound community level, in structuring arboreal herbivore faunas in rain forests. The selective advantages of monophagy are likely to be high, providing that (a) the overall chemical diversity of the rainforest plant community is high and (b) that the herbivore community associated with a particular host-tree confront well-developed and diversified chemical defences which are distinct from those exhibited by the rainforest plant community as a whole. Referring to the latter, Cornell (1989) suggested that endophage-ectophage ratios of folivores should increase on more heavily defended hosts, implying that the load of specialists should be high on these hosts.

On *A. actinophyllum*, the abundance of mucilage canals and cells (which induce gum production) explains, in part, the low proportion of chewing species in

comparison with that of sap-feeding species, which can avoid more easily this type of defence (Basset, 1991a). Other identified chemical and structural traits of the foliage of this tree include low nitrogen (young leaves : 1.8% DW; mature leaves : 1.6% DW) and water content (mature leaves : 53% FW), high fibre content (mature leaves : 55% DW), relatively high toughness (specific leaf weight of mature leaves: $100.9 \times 10^{-4} \text{ g cm}^{-2}$) (Basset, 1991d; levels of total phenols and tannins not determined), absence of alkaloids (Webb, 1952), and probable absence of cyanogenic compounds, as reported for a close species, *A. trifoliolatum* (Webb, 1949). This apparent scarcity of qualitative defences, and, equally important, the low nutrient content (see Mattson & Scriber, 1987 for a discussion about the range of values of variables affecting food quality) are not likely to select strongly for a specialist strategy among herbivores.

A second and major selection pressure may influence feeding strategies of rainforest herbivores towards restricted host range. Bernays & Graham (1988) argued that generalist predators provide such a pressure, which may even be more important than chemical defences, since reduction in losses to predation may be achieved through morphologies and behaviours which are particularly appropriate for a narrow range of hosts. Further, Thomas (1989) suggested that the high botanical diversity of rain forests may be maintained by a preponderance of generalist predators. In some instances, high predation risks may favour either concealment in the tissues of the host, or a reproductive strategy focusing on a few hosts. For example, the specialized diet of certain *Heliconius* butterflies on their *Passiflora* hosts appears to result from the predation pressure exerted by ants on butterfly eggs (Smiley, 1978). Arboreal ants exert a considerable predation pressure in most rain forests (as judged by their numerical importance), but not in Australian rain forests (review in Majer, 1990), and similarly, not on *A. actinophyllum*, where the seasonal and relatively unpredictable production of young foliage limits the successful foraging of ants for herbivore prey (Basset, 1991a; ants amount to 2.0% of total individuals and 0.6% of total arthropod biomass collected by fogging). On this tree, spiders have filled the vacant niche, but probably not with the same success as ants, since they avoid young foliage patches with rich aggregations of herbivores (Basset, unpublished). Although a compensatory predation pressure, which may be exerted by other insect predators/parasitoids and vertebrate predators, cannot be excluded, the relatively low ant predation pressure on *Argyrodendron actinophyllum* may decrease the importance of enemy-free space in the evolution of feeding strategies of associated herbivores.

SELECTION PRESSURES SHAPING POLYPHAGY IN RAIN FORESTS

Generalized models about the evolution of specialization predict that the probability of this strategy augments with a decrease in the cost of search, and with an increase in the relative abundance of the host (Futuyma & Moreno, 1988). Accordingly, the botanical diversity of rain forests represents a major structural constraint upon herbivores. The location of suitable young foliage by rainforest herbivores on specific hosts is usually costly and dispersal is hazardous and problematic. Therefore, this type of constraint should favour polyphagy (Beaver, 1979), provided it is chemically feasible. However, the abilities of herbivores to locate and colonize a suitable host in rain forests may be quite

different between phytophages. For example, Dixon *et al.* (1987) explain the difference between relative success of rainforest Psylloidea and the scarcity of rainforest Aphidoidea in terms of their different adult life-spans. Aphids have shorter life-spans than psyllids and have a more limited supply of energy at disposition for host location since they must often sustain polyembryonic larvae. Other specialized and short-lived phytophagous insects during the dispersal phase, such as certain Symphyta, appear to be uncommonly sampled in the tropics (e.g. Gauld, 1986). It is difficult to appreciate the contemporary problems that herbivores encounter in locating *A. actinophyllum*. This tree is one of the dominant canopy species in warm subtropical rain forests of Australia (McDonald & Whiteman, 1979). At Mt Glorious, walking anywhere in the rain forest for 15 minutes will result in the sighting of at least one individual belonging to this species. Although the subjective impression suggests that host location may not be difficult in these conditions, the extent to which these considerations apply to insect herbivores is not known.

It is certain that environmental unpredictability represents an important and powerful force in the evolution of polyphagy (Futuyma, 1976). Populations of generalist species tend to be less variable than those of specialists, since they may be less susceptible to fluctuating resource levels (e.g. Redfearn & Pimm, 1988). Earlier anecdotal accounts emphasized rain forests as relatively stable ecosystems, providing steady food resources for insect herbivores. Subsequently, it has been shown that tropical insect populations fluctuate, occasionally as much as in temperate conditions, in response to their changing and sometimes unpredictable environment (e.g. Bigger, 1976; Wolda, 1978; Basset, 1991b). Although abiotic factors in rainforest environments may be relatively stable, it does not necessarily imply that herbivore food resources follow a similar trend. Rather, food supply is likely to be a function of young foliage availability, and therefore, of host phenology (see below). Terborgh (1986) even argued that the more uniform the climate, the more unpredictable and irregular will be the production of resources by tropical vegetation. Michaud (1990) proposed that intraspecific variation in host quality may be an important factor for the evolution and maintenance of polyphagy. Little is known about the degree of intraspecific differences in foliage quality of rainforest trees but, presumably, they are high, since, for example, distinct parts within a tree crown may experience marked differences in young foliage abundance, illumination regime, relative humidity, wind exposure etc. Thorough studies by Langeheim & Stubblebine (1983) showed that intrapopulation variation in sesquiterpenes for *Hymenaea* spp. trees are greater in rainforest sites than in savanna sites. However, in this case, resin composition is under tight genetic control and varies little with environmental factors, although its total yield does (Langenheim & Stubblebine, 1983). Most of intra-crown variability in leaf traits which have been measured for *A. actinophyllum* seems to be induced by illumination regime (Basset, unpublished).

Rainforest herbivores encounter significant energetic constraints, since the limiting factor for herbivore growth and fecundity, foliar nitrogen, is usually found in much lower levels within evergreen rainforest foliage than within deciduous temperate foliage (Mattson, 1980). Most rainforest herbivores aggregate and feed upon young leaves (e.g. Coley, 1983; Aide & Londoño, 1989; Basset, 1991b, 1991d), partly because their content in nitrogen is usually higher

than that of mature foliage (Mattson, 1980). The importance of these energetic constraints should not be underestimated, since (a) herbivores of nutrient-impooverished plants tend to be more polyphagous than those associated with nutrient-rich plants (Mattson & Scriber, 1987); and (b) some rainforest herbivores favour skeletal economy in response to their poor diet (Rees, 1986). Thus, polyphagy may be a widespread strategy among free-living folivores feeding upon particularly nutrient-poor rainforest trees, such as *A. actinophyllum*.

Concurrent with this view, the costs to herbivores for location of host and suitable young foliage are likely to depend significantly on host phenology, which is often complex in rain forests (e.g. deciduous or evergreen; intermittently or continuously flushing; intraspecific synchronous or asynchronous leaf production between or within crowns; leaf flush total dependent on external environmental factors etc; see Frankie, Baker & Opler, 1974; Opler, Frankie & Baker, 1980). Since these complex combinations may establish a larger overlap of leaf-flushing periods in rain forests than in temperate forests, availability of young foliage should be higher for generalists than for specialists, provided that generalists are able to tolerate or overcome the chemical protection of young leaves. Conversely, a continuous and stable food supply, represented by the continuous leafing of certain rainforest trees, may favour a specialized diet among associated herbivores. *Argyrodendron actinophyllum* is an intermittently growing evergreen whose marked yearly differences in leaf turnover renders young foliage relatively unpredictable to specialist herbivores (Basset, 1989, unpublished). In these conditions, host location costs are presumably high and should favour (a) highly specialized herbivores able to adapt closely to their host phenology, such as the psyllids *Aconopsylla* sp. and *Protyora* sp., which feed upon both vegetative and reproductive meristems in order to short-circuit the escape in space and time of vigorous *A. actinophyllum* trees (Basset, 1989, unpublished); and (b) a relatively low proportion of such specialized species.

Lastly, abiotic factors may exert some influence on the evolution of feeding strategies among rainforest herbivores. High air temperatures, for example, increase the occurrence of insect flights (e.g., Basset, 1991b), and this high activity may further optimize polyphagy. High rainfall evenly distributed throughout the year may enhance fungal growth and attack, which may be to the detriment of concealed feeders and sedentary herbivores rather than external and mobile feeders, thus promoting polyphagy to some extent. Indeed, gall-makers are abundant in xeric sites and relatively scarce in rain forests, but the cause of this observation is unclear (Fernandes & Price, 1988), and therefore, the above hypothesis remains highly speculative.

HOST SPECIFICITY OF INSECT HERBIVORES IN RAIN FORESTS: A TENTATIVE CONSPECTUS

At the moment, no formal testing of the host specificity of arboreal and free-living folivores has been yet published. This is probably due to the formidable physical constraints upon insect sampling and canopy access in rainforest environments, not to mention concomitant problems of insect identification. At this stage of research, we must rely on indirect information to hypothesize upon the host-specificity of rainforest herbivores.

The rainforest compound community plays a key role in the shaping of

herbivore feeding strategies, but the importance of attributes inherent to component communities (the host-trees and their associated fauna) should not be neglected, as documented in the present study. *Argyrodendron actinophyllum* is a climax species, whose foliage is characterized by low nitrogen and water content, high fibre content and absence of alkaloid and, therefore, falls into the rainforest tree category which is protected by dose-dependent quantitative defences (Waterman & McKey 1989). These chemical features appear not to pressure herbivores strongly toward the adoption of monophagy. For a converse example, the associated beetle fauna of *Luehea seemannii* appears to include many specialized species. Foliar characteristics are quite distinct between *Luehea* and *Argyrodendron*, the former tree being a pioneer species, with high nutrient and water levels and low fibre content (mature leaves: 2.6% N, 59% water, 33% fibre: Coley, 1983). These two trees may represent different directions (namely qualitative and quantitative) in a continuum of defensive characteristics for rainforest trees (Waterman & McKey, 1989), which may influence in different ways respective loads of associated herbivores. Similarly, several studies emphasize the role of chemical traits of the host in shaping the feeding strategies of associated herbivores. In Costa Rica, Saturniidae, which prefer host plants rich in tannins and fibre and deficient in water, are less host-specific than Sphingidae, which feed preferentially on hosts containing alkaloids or other qualitative defences (Janzen & Waterman, 1984; Waterman & McKey, 1989). Most caterpillar species of a Costa Rican deciduous forest were found by Janzen (1988) to be highly specialized. Foliar levels of nitrogen and fibre are, respectively, usually higher and lower in deciduous tropical trees than in evergreen rainforest trees (Mattson, 1980; Coley, 1983; Janzen & Waterman, 1984; Waterman & McKey, 1989). However, Janzen did not state explicitly the ratio of polyphagous species in external feeders. The Dipterocarpaceae from lowland rain forests of South-East Asia support very few lepidopteran defoliators and most of them are polyphagous (Holloway, 1989). Usually, these host-trees exhibit high fibre and low nitrogen contents (mean of 11 species: 1.8% N, 58% fibre; Waterman *et al.*, 1988).

Janzen (1985) stated that the more a plant relies on a purely polyphenol defence system, the more it would appear to be susceptible to generalist feeders such as saturniid moths. Incidentally, several authors suggested that the role of polyphenols as quantitative defences, and particularly that of tannins, may have been overemphasized in comparison with that of fibre (Coley, 1983; Waterman & McKey, 1989). In herbaceous plants, the greater the chemical complexity of the hosts, the greater the degree of specialization of insects associated with them (Berenbaum, 1981). The extent to which this relation may hold for woody plants and their associated insects is not known. In some instances, correlations between soil nitrogen and the production of secondary substances such as alkaloids (a class of nitrogen-containing toxins) have been demonstrated (Berenbaum, 1981). Usually, poor nutrient availability favours reduced growth rate of plants and high investment in defence (Janzen, 1974; Coley, 1983; Coley *et al.*, 1985), with non-nitrogen-based allelochemicals (i.e. most defences defined as 'quantitative'), unless plants can rely upon nitrogen-fixing symbionts (Mattson, 1980; it is not known whether *A. actinophyllum* is a mycorrhizal species). However, the chemical diversification of carbon-based defences within plants growing on impoverished soils appears to be lower than that of nitrogen-based defences within plants

growing on rich soils (Mattson, 1980). Alternatively, there may exist a lower threshold where resource limitation may promote low nutritive quality itself as a defence, in prolonging herbivore growth and, therefore, herbivore exposure to predators, for example (Moran & Hamilton, 1980).

In addition, there is growing evidence that such differences in chemical defences and nutrient levels between rainforest-tree species may also exist between different types of rain forest (Waterman & McKey, 1989). For example, some African rain forests grow on poorer nutrient sites than others and their respective chemical features differ accordingly (Waterman & McKey, 1989). A distinctive feature of Australian ecosystems, and of Australian rain forests, are low-nutrient soils (Westoby, 1988). If a substantial proportion of the botanical community relies upon the same type of defences, which are not extremely diversified (i.e. carbon-based quantitative defences), driven, for example, by a poor nutrient availability, the occurrence of polyphagy within the herbivore community may be enhanced.

However, it is certainly an oversimplification to conclude that the host specificity of rainforest arboreal herbivores may covary with the composition of chemical defences and the nutrient levels of their hosts, as ultimately suggested both by the resource availability (Coley *et al.*, 1985) and the plant apparency theories (e.g. Feeny, 1976). The former fails to recognize the importance of host abundance *per se*, which may be crucial in some instances (e.g. Smiley, 1978), and subtle but important differences in host phenology, which may not be accounted for by general differences in host growth strategy (i.e. pioneer/climax species), while several problems are involved with the latter (Fox, 1981; Barbosa, 1988). Furthermore, in both cases the role of herbivore predators/parasitoids in herbivore diet specialization have been ignored (review in Barbosa, 1988).

In case of marked differences in chemical defences and nutrient levels between young and mature foliage, seasonal trends of host foliage production may influence considerably herbivore diet choice. The study of *A. actinophyllum* adds some support to this view, since (a) host utilization by most herbivores was restricted temporally to periods of young foliage availability and (b) arthropod assemblages were random on the mature foliage, whereas arthropod clusters were more predictable on young foliage, following aggregation of herbivores on a favourable food resource (Basset, unpublished). Since nitrogen-rich young foliage, appears to affect significantly herbivore distribution on nutrient-poor rainforest trees such as *A. actinophyllum* (Basset, 1991d), the cohesion of the arboreal community may, in some instances, depend on the leaf production pattern of the host. Predictable interactions with the host, particularly on an ecological scale, are a prerequisite for the occurrence of coevolution (Craig *et al.*, 1988), and, ultimately, for the speciation of specialized herbivores. Accordingly, rainforest evergreen tree species, which disclose a relatively continuous leaf production, may reveal high proportions of associated specialist chewers. In contrast, intermittently growing evergreens may sustain more phloem-feeder specialists, since those are strongly influenced by young foliage production and the concomitant nitrogen translocation (Basset, 1991d). Furthermore, in some tropical rain forests, referred to as single-dominant forests, 50–100% by number of canopy trees belong to one species (reviewed in Connell & Lowman, 1989). In these forests, both the overall structural diversity and the high apparency of dominant species are likely to affect the diet specialization of insect herbivores significantly.

Lastly, the importance of enemy-free space should not be underestimated. Smiley (1978) showed that, occasionally, monophagy could evolve initially as a result of predation pressure or plant abundance, and then be maintained by differences in host palatability.

SUMMARY

Argyrodendron actinophyllum presents several features which may promote a polyphagous strategy among herbivores: low nutrient levels and high fibre content, apparent scarcity of qualitative defences, relatively unpredictable availability of young foliage and low predation-pressure from arboreal ants in its foliage. This situation may be different for other rainforest tree species, depending on their biological features. Without speculating on the relative importance of each factor, these observations suggest that the strength of association between communities of insect herbivores and their rainforest host-trees may depend on the following factors, acting at both the component and compound rainforest-community level: chemical traits of foliage (including chemical defences and nutrient levels), young foliage availability (including factors related to plant phenology, plant abundance and plant growth strategy) and enemy-free space. These factors, which may be interrelated (i.e. amount and type of chemical defences related to nutrient availability, host phenology related to nutrient availability and searching behaviour of generalist predators/parasitoids related to host phenology and apparency), may generate complex sets of combinations, which are likely to differ between rainforest component communities. In these conditions, rainforest host-trees may sustain herbivore faunas ranging from highly specialized to highly generalist. These considerations demonstrate a requirement for the study of arboreal insect communities associated with host-trees of dissimilar features growing in similar rain forest types, as well as in different rainforest environments.

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