

Host-specificity of folivorous insects in a moist tropical forest

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Summary

1. To assess the degree of herbivore host-specificity in the moist tropical forest on Barro Colorado Island, Panama, I conducted an extensive series of feeding trials on the common insect herbivores from 10 tree species.

2. The herbivores were offered leaves from both congeneric and confamilial plant species to their known host species, as well as leaves from the most abundant tree species in the forest.

3. The amount of damage caused by these herbivores to young, expanding leaves was also measured on nine of the tree species.

4. Of 46 herbivores species (seven Coleoptera, one Orthoptera, 38 Lepidoptera), 26% were specialized to a single plant species, 22% were limited to feeding on a single genus and 37% were able to feed on several genera within a single family. The remaining 15% were generalists, able to feed from several different plant families.

5. The causes of leaf damage varied extensively across the tree species. On average, specialist herbivores caused 58% of the damage to young leaves, generalists herbivores 8% and fungal pathogens 34%. For four of the tree species, pathogens were the most important cause of leaf damage.

6. In this forest, most chewing herbivores appear to have fairly narrow diets, and these specialists are responsible for most of the insect herbivory.

Key-words: Barro Colorado Island, diet specialization, herbivores, herbivory, pathogens.

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Introduction

An understanding of the host-specificity of herbivorous insects in tropical forests is critical to answering numerous ecological questions, including several related to species diversity. For example, recent assessments of global species richness have been based on largely untested estimates of the degree of herbivore specialization of tropical forest arthropods (Erwin 1982; Stork 1988). In addition, one proposed explanation for the high species diversity of tropical forests argues that, compared those in the temperate zone, organisms in the tropics have narrower niches, allowing more species to be packed together in a given habitat (MacArthur 1969). Because insect herbivores usually reside on their food plants, their niche breadths may be measured in part by their diet breadths. Thus, details on the degree of host-specificity of temperate and tropical insects would provide one way to evaluate MacArthur's hypothesis. Finally, more information on the host-specificity of herbivores is necessary to evaluate another prominent diversity

hypothesis, the Janzen–Connell model of tropical tree diversity (Janzen 1970; Connell 1971). Janzen and Connell argued that seed predators, herbivores and pathogens maintain local tree diversity by causing disproportionately high rates of mortality of seeds and young trees growing near conspecific adults, suppressing the density of competitively dominant species and allowing more tree species to co-exist. An explicit assumption of this model is that these natural enemies have narrow diet ranges.

Despite the importance of understanding the host-specificity of tropical herbivores, the issue has received relatively little attention (Basset 1992). Most studies have determined the diet breadths of herbivorous insects based on collection records (e.g. Wood & Olmstead 1984; Janzen 1988; Hodkinson & Casson 1991). Though this method can be very effective, its accuracy depends upon the extent of the records. Furthermore, such studies typically present host specificity from the herbivore's perspective, reporting the number of plant species or families that a particular taxonomic group can consume (Basset 1992), e.g. the

average number of plant families that caterpillars in the Geometridae can eat. An alternative approach is to examine the degree of diet specialization of herbivores that attack a particular plant species (Basset 1992). Some plant species may be attacked mainly by generalist herbivores, whereas others may only be susceptible to a group of specialists. Though both approaches are valuable, the second is preferable when the main concern is the impact of the herbivores on plants, either at the individual, population or community level.

In this study, I evaluated the host-specificity of chewing insect herbivores collected from 10 tree species in a lowland tropical forest in Panama, using an extensive series of feeding trials. In addition, the relative amounts of leaf damage caused by specialist and generalist herbivores, as well as fungal pathogens, were also measured. Documenting the damage by herbivores with different diet ranges is important, because the impact of herbivores depends not only the proportion of species with a given host range, but also upon the amount of damage they do.

Methods

STUDY SITE AND SPECIES

This research was conducted on Barro Colorado Island (BCI) (9°09'N, 79°51'W), which is part of the Barro Colorado Nature Monument in the Republic of Panama, and site of a field station operated by the Smithsonian Tropical Research Institute. The island receives 2600 mm of rainfall annually and experiences a single long dry season from mid-December until April (Windsor 1990). The vegetation on BCI is classified as moist or semi-deciduous lowland tropical forest and is quite diverse, with at least 1300 plant species, including 356 species of trees (Holdridge *et al.* 1971; Croat 1978; Foster & Brokaw 1982). The island has a mix of secondary forest dating from the 1880's and mature forest that is at least 300–400 years old (Foster & Brokaw 1982). Leigh, Rand & Windsor (1982) and Gentry (1990) contain details on the climate and natural history of BCI.

The feeding trials were conducted on insects from 10 species of canopy or subcanopy trees (Table 1) which, for convenience, I will refer to as the 'focal' plant species. Eight of the 10 are among the 20 most abundant woody species on the 50-ha Forest Dynamics Plot on BCI (see Hubbell, Condit & Foster 1990 for a description) and together account for 40.3% of the stems of tall and medium-sized tree species (Condit, Hubbell & Foster 1996). Two species are rarer. *Prioria copaifera* Griseb. a canopy tree, has a clumped distribution, with most individuals on BCI growing in the mature forest on wet slopes or close to the island's edge (Croat 1978). *Hirtella americana* L. is uncommon in both the young and mature forest (Croat 1978). Overall, these 10 species were chosen because they

represent a diverse array of plant families and have been the subject of numerous ecological studies that provide useful background information (e.g. Leigh *et al.* 1982; Coley 1983; Hubbell *et al.* 1990; DeSteven 1994). Some of the species were also selected because they are related (i.e. three species in the family Burseraceae, two species in the genus *Hirtella*) in order to examine the extent of the overlap of their herbivore faunas.

COLLECTION AND CARE OF HERBIVORES

The herbivores used in the feeding trials were collected by hand in a haphazard fashion during other work in the forest as well as during specific herbivore searches. Individuals of each species were reared to maturity (when necessary) and preserved for identification. All herbivores were identified at least to the family level. As specimens are identified, vouchers are being deposited at the Fairchild Museum, University of Panama, in Panama City, Republic of Panama.

Collections were made during a cumulative period of over 2 years, from September 1992 to November 1995. All of the herbivores were maintained in a screened room subject to ambient conditions, though a black plastic curtain protected them from direct sunlight. Each herbivore had its own container, either a clear plastic Petri dish (9 × 1.5 cm), a larger, clear round dish (9 × 6 cm) or, in a few cases, an opaque, round container (12 × 9 cm) with partly screened lid. A small, damp piece of paper towel was placed in each dish to help maintain humidity. Between trials, fresh, edible leaves were provided daily and frass was removed. Each container was scrubbed routinely with dish soap and, following the death of a herbivore from a pathogen infection, the container was also rinsed with a 1:1 solution of bleach and water.

FEEDING TRIALS

To determine diet breadth, each herbivore species was presented with leaves from an alternative plant species, using a no-choice design. Only shade leaves from the understorey were used in the trials, and they were harvested daily, placed in a sealed plastic bag with a wet paper towel and typically given to the herbivores within 2 h of being collected. All trials lasted 24 h, and were usually started in the late afternoon or early evening. When the leaf was not eaten at all or received only one or two bites, it was considered to be inedible to the herbivore. If the herbivore took more than a few bites, the leaf was recorded as being edible. In the vast majority of cases, herbivores either ate the leaf extensively or ignored it completely. A trial was voided if the herbivore moulted or pupated and left the leaf untouched, as insects frequently cannot eat during these periods.

The alternative plants tested in the feeding trials form two groups: (1) those related to the focal plant

Table 1. Focal tree species and species used in feeding trials. Names follow Croat (1978) except *Trichilia tuberculata* (= *cipo*). None means that no congeneric species are present in the BCI forest. Abundant tree species are listed in descending order of abundance (Condit *et al.* 1996)

Focal species (Family)	Congeneric species	Confamilial species	Abundant species
<i>Alseis blackiana</i> (Rubiaceae)	None	<i>Alibertia edulis</i> <i>Coussarea curvigemma</i> <i>Faramea occidentalis</i>	<i>Quararibea asterolepis</i>
<i>Hirtella americana</i> (Chrysobalanaceae)	<i>Hirtella racemosa</i> <i>Hirtella triandra</i>	<i>Licania hypoleuca</i> <i>Licania platypus</i>	<i>Trichilia tuberculata</i>
<i>Hirtella triandra</i> (Chrysobalanaceae)	<i>Hirtella americana</i> <i>Hirtella racemosa</i>	<i>Licania hypoleuca</i> <i>Licania platypus</i>	<i>Alseis blackiana</i>
<i>Prioria copaifera</i> (Fabaceae)	None	<i>Swartzia simplex</i> <i>Tachigalia versicolor</i>	<i>Prioria copaifera</i>
<i>Protium panamense</i> (Burseraceae)	<i>Protium costaricense</i> <i>Protium tenuifolium</i>	<i>Tetragastris panamensis</i>	<i>Hura crepitans</i>
<i>Protium tenuifolium</i> (Burseraceae)	<i>Protium costaricense</i> <i>Protium panamense</i>	<i>Tetragastris panamensis</i>	<i>Faramea occidentalis</i>
<i>Quararibea asterolepis</i> (Bombacaceae)	<i>Quararibea pterocalyx</i>	<i>Ceiba pentandra</i> <i>Ochroma pyramidale</i> <i>Pseudobombax septenatum</i>	<i>Ceiba pentandra</i>
<i>Tachigalia versicolor</i> (Fabaceae)	None	<i>Prioria copaifera</i> <i>Swartzia simplex</i>	<i>Anacardium excelsum</i>
<i>Tetragastris panamensis</i> (Burseraceae)	None	<i>Protium costaricense</i> <i>Protium panamense</i> <i>Protium tenuifolium</i>	<i>Beilschmiedia pendula</i>
<i>Trichilia tuberculata</i> (Meliaceae)	<i>Trichilia pallida</i>	<i>Guarea guidonia</i> <i>Guarea grandifolia</i>	<i>Jacaranda copaia</i>

species; and (2) the most abundant tree species on BCI (Table 1). First, each herbivore species was tested on young and mature leaves of all the common congeners of its focal species on BCI. Next, tests were conducted using plants from the same family as the focal species. For some plant families, such as the Chrysobalanaceae, that have only a few species on BCI, all the species were tested. For families with numerous species (e. g. Rubiaceae and Fabaceae), I selected two or three tree species that were common in the forest. Finally, each herbivore species was tested against the young and mature leaves of 10 of the most common tree species on the island (Table 1). Together, these 10 tree species account for 51.8% of the stems and 44.0% of the basal area of medium and tall trees, based on the censuses of the 50-ha plot (Condit *et al.* 1996). By testing these species, I could eliminate a large proportion of the trees on the island as potential hosts for the herbivores. Moreover, they represent a diverse cross-section of the plant families and orders in the forest.

Each individual herbivore was fed the young or mature leaves of a test plant species a single time. This means that for any particular plant species, each trial was independent with respect to the herbivores. Some individual herbivores, however, were used in trials for more than one plant species, potentially confounding the results across species. For example, if a few individuals of a rather specialized herbivore species had an atypically broad diet in the trials, their species would be classified inappropriately. I strongly doubt

that this problem ever occurred during the course of this study for two reasons. First, for a given herbivore species, all of the individuals typically displayed very similar preferences. Secondly, most individuals were used in only a few trials before they pupated, died or were released, lessening the impact of any individual. One solution to this type of problem is to use each individual herbivore in only a single trial, but that was unrealistic in this setting because not enough herbivores could be found.

For a particular herbivore species, a plant species was only excluded as a possible host if, in doing so, the chance of making an error was less than 5% ($P < 0.05$). For example, if in seven trials, one individual herbivore of a species could eat the plant ($P = 0.055$ in a binomial distribution), then the plant was not excluded and was instead considered to be a host plant. This standard was employed because, based on the literature, I expected that specialists would be more common than generalists and thus designed the tests to detect generalists. Consequently, this study may over-estimate the number of generalist species on BCI.

HERBIVORY AND DEGREE OF SPECIALIZATION

During this study, I learned to recognize the types of leaf damage left behind by the herbivore species that feed on the 10 focal plant species. I used this familiarity to determine the relative amounts of damage caused by herbivores with different diet breadths.

Approximately 50 saplings (0.2–2.0 m tall) of each of the 10 tree species were marked in August and September 1994. In the early wet season (April–June) of 1995, I tagged young leaves on these saplings as they emerged from their buds, by winding a small piece of coloured wire on a nearby shoot or mature leaf, and counting the number of nodes between the wire and the new leaf. I measured herbivory on young leaves because rates of herbivory are higher on young than mature leaves, and a majority of a leaf's lifetime damage typically occurs during the period of leaf growth and expansion (Coley 1980, 1983; Coley & Kursar 1996). When the leaves had matured (between 3 and 6 weeks later depending on the species), herbivory was measured by placing a small, clear plastic grid over each leaf, and counting the number of squares of both the leaf and the area of damage. When a leaf was completely eaten, damage was scored as 100%. For each leaf that was still attached to the plant, the herbivory was attributed to a particular herbivore species on the basis of the pattern of damage. The one exception was leaf damage to *Trichilia tuberculata* C. DC. which is attacked by several herbivore species that cause very similar types of damage.

DEFINITIONS

Different authors have defined the terms associated with the degree of herbivore specialization, such as monophagous or polyphagous, in strikingly varied ways (Strong, Lawton & Southwood 1984). For clarity, I use the following terms. A 'species-specialist' is a herbivore species that can feed only on a single plant species. Likewise, a 'genus-specialist' is limited to plants from one genus, and a 'family specialist' is restricted to plants from a single family. 'Specialist' by itself refers to the sum of these three categories (i.e. herbivores that feed at the most on species from one plant family) and a 'generalist' is any herbivore species that can feed on species from more than one plant family.

Results

FEEDING SPECIALIZATION

During the course of the study, more than 4000 herbivores were collected and just over 7000 individual feeding trials were conducted. In total, 151 species of chewing herbivores were found to feed on at least one of the 10 focal species, ranging from six species on *Tachigalia versicolor* Standl. & L.O. Wms. to 34 species on *Hirtella triandra* Sw. The collections included seven species of Orthoptera, 14 Coleoptera and 130 Lepidopteran larvae. Of the 151 species, 90 were collected only one or two times.

The results reported here are based on the feeding trials of 46 herbivore species, which were the most

Table 2. Families of the 46 herbivore species used in the feeding trials. Classification follows Stehr (1987)

Family	Species	Family	Species
Lepidoptera			
Arctiidae	3	Pyralidae	5
Ctenuchidae	1	Sphingidae	1
Gelechiidae	2	Thyrididae	1
Geometridae	2		
Hesperiidae	3	Coleoptera	
Limacodidae	1	Cerambycidae	1
Megalopygidae	1	Chrysomelidae	2
Noctuidae	7	Curculionidae	3
Notodontidae	3	Undetermined	1
Nymphalidae	2		
Oecophoridae	5	Orthoptera	
Pterophoridae	1	Acrididae	1

common species on the focal plants. Lepidoptera larvae from 15 families were represented in the trials, along with four families of Coleoptera and one family in the Orthoptera (Table 2). For 29 of the species, the feeding trials were completed or nearly completed. I also include the results for the remaining 17 species, even though the trials were incomplete, because the degree of host-specificity was evident, based on both field observations and the results of the trials. In particular, there was no instance where an herbivore accepted confamilials of its host species, but rejected more closely related plant species.

Of the herbivores tested, 48% were either species-specialists or genus-specialists (Fig. 1) and only 15% were generalists. Though narrow diets were common, the degree of host-specificity of herbivores varied across plant species (Table 3). For example, five herbivore species collected from *Alseis blackiana* Hemsl. were species-specialists, though five of the seven species of generalist herbivores were also found on this tree species. In contrast, five of the focal tree species harboured no species-specialists at all.

Eleven of the herbivore species (24%) were young-leaf specialists, meaning that they could only consume young leaves, or in the case of some caterpillar species, that they required young leaves for the first few

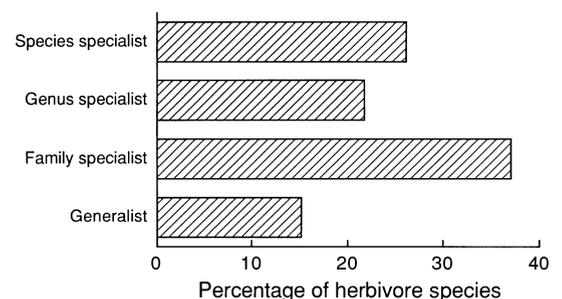


Fig. 1. Host-specificity of chewing herbivores based on the feeding trials. $n = 46$ species. See text for definitions.

Table 3. Host-specificity of herbivores from feeding trials. Note that the total herbivore species do not add up because in some cases the same species of herbivore was collected from more than one focal plant species. Specialization refers to the broadest category applicable to a species. For example, a family specialist can eat plants from more than one genus within a plant family, but no plants outside of that family. Age specialist refers to herbivores which can only feed on leaves at a particular developmental stage

Focal plant species	Degree of specialization				Age specialist	
	Species	Genus	Family	Generalist	Young	Mature
<i>Alseis blackiana</i>	5	0	0	5	0	0
<i>Hirtella americana</i>	0	3	3	0	1	0
<i>Hirtella triandra</i>	0	2	5	3	1	0
<i>Prioria copaifera</i>	2	0	0	0	2	0
<i>Protium panamense</i>	0	2	0	1	2	2
<i>Protium tenuifolium</i>	1	0	4	0	2	1
<i>Quararibea asterolepis</i>	0	5	4	4	2	0
<i>Tachigalia versicolour</i>	2	0	0	2	1	0
<i>Tetragastris panamensis</i>	0	0	1	1	1	0
<i>Trichilia tuberculata</i>	2	0	4	2	1	0
Total herbivore species	12	10	17	7	11	3

instars. Three species of mature-leaf specialists were also collected, all of them from plants in the genus *Protium* (Table 3). The remaining 35 herbivore species were able to consume either young or mature leaves at any time during their development.

As I mentioned, the rarity of many herbivore species precluded them from being adequately tested in the feeding trials. Nevertheless, based on the limited feeding trial data and some field observations, I have classified all the species I possibly could as specialists or generalists. Out of 104 species, 57 (55%) were specialists and 47 (45%) were generalists. I consider these classifications to be very tentative and they may not represent the herbivore community as a whole. In addition, as I discuss below, the sampling method used in this study is likely to be biased toward finding generalists.

HERBIVORY AND HOST-SPECIFICITY

The average leaf area damaged on the marked saplings varied from 12% on *A. blackiana* to 87% on *Tetragastris panamensis* (Table 4). The amount of damage

Table 4. Proportion of damage to young leaves of the focal tree species. *n* = number of saplings measured

Species	Average area lost	SE	<i>n</i>
<i>Alseis blackiana</i>	0.12	0.040	40
<i>Hirtella americana</i>	0.25	0.064	40
<i>Hirtella triandra</i>	0.28	0.062	28
<i>Prioria copaifera</i>	0.54	0.10	15
<i>Protium panamense</i>	0.31	0.081	24
<i>Protium tenuifolium</i>	0.50	0.11	20
<i>Quararibea asterolepis</i>	0.25	0.065	23
<i>Tachigalia versicolour</i>	0.27	0.097	19
<i>Tetragastris panamensis</i>	0.87	0.047	34
<i>Trichilia tuberculata</i>	0.19	0.055	31

did not correlate with the number of specialist or generalist herbivore species on a tree species. The relative amounts of damage caused by specialist and generalist herbivores, as well as pathogens, are shown in Fig. 2. The proportion of damage caused by different groups varied considerably across the tree species, but specialist herbivores caused more damage than did generalists in all but one case. The exception, *T. versicolour*, is a species that experiences relatively little damage from insects. Averaged across all the tree species, 58% of the leaf damage was caused by specialist herbivores, 8% by generalists and 34% by pathogens, all of which appeared to be fungal. Of the herbivory by insects, specialists caused seven times more damage than generalists.

Discussion

HERBIVORE SPECIALIZATION

In the lowland tropical forest of BCI, almost half of the species of chewing herbivores examined had a very narrow diet, limited to a single genus and only 15% were able to feed on plants from more than one family. In addition, the majority of the insect damage to leaves was due to specialized herbivores.

The degree of host-specificity found in this study agrees fairly well with most other studies of chewing herbivores. Based on extensive collections, Janzen (1988) estimated that about half of the caterpillar species in a dry forest in Costa Rica are restricted to feeding on a single plant species and that generalist species were quite rare. Several different insect groups have also been shown to have narrow diets in the tropics. Ithomiine and *Heliconius* (Nymphalidae) caterpillars typically feed on one to three host-plant species (Benson 1978; Drummond 1986; Brown 1987) in the Neotropics. Most Hemiptera in Dumonga Bone

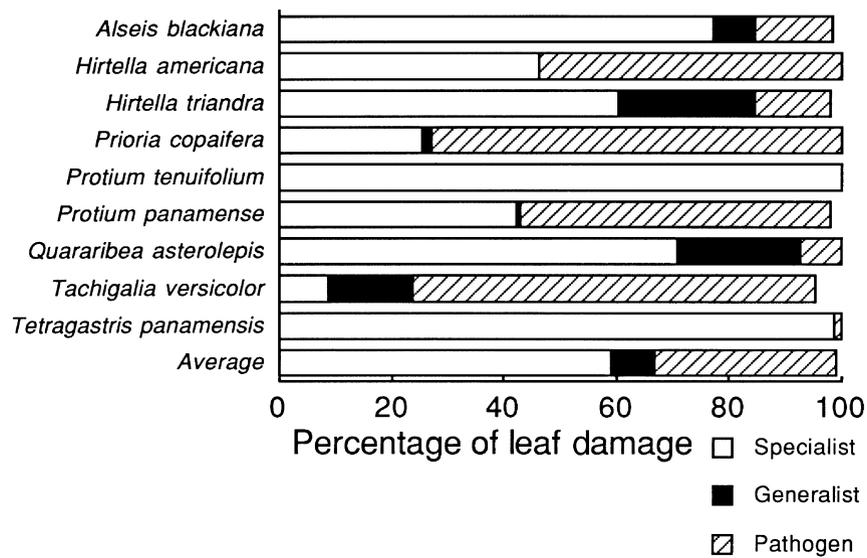


Fig. 2. Percentages of damage to leaves of the focal tree species by insect herbivores and pathogens. Average is the mean for the nine tree species. The bars do not all reach 100% because of damage from falling branches and unknown causes. *Trichilia tuberculata* was excluded because of the similarity of damage by several species of herbivores.

National Park, Indonesia, are restricted to hosts from a single plant family (Hodkinson & Casson 1991).

Marquis (1991) conducted lengthy censuses of the herbivores attacking *Piper* shrubs in the wet forest at La Selva, Costa Rica, and was able to determine the host range of the weevils and geometrids attacking this genus. He found that 71% of the geometrids and 48% of the weevil species fed on only one or two species of *Piper*. To explain the difference between the two herbivore groups, Marquis argued that weevils may be more generalized because they are poorer dispersers and less likely to find rare hosts.

In contrast to these studies, Basset (1992) censused herbivores on the tree *Argyrodendron actinophyllum* (Sterculiaceae) in a subtropical forest in Australia, and found that only 11% of the herbivores (out of 156) were specialists. Because of a sampling problem detailed below, I believe that this study greatly overestimates the proportion of generalist species in this forest and thus does not contradict the other studies that have found relatively high levels of specialization in tropical herbivores.

Comparative studies between temperate and tropical regions also suggest that insect herbivores may have narrower diets in the tropics. For example, caterpillars from three families (Papilionidae, Pieridae and Nymphalidae) have narrower host-ranges in the wet forest at La Selva than at five temperate sites (Marquis & Braker 1994). The same latitudinal pattern exists for grasshoppers (Marquis & Braker 1994). Scriber (1973) likewise showed that species in the Papilionidae at lower latitudes had narrower diets than did more temperate species.

Together with the present findings, these studies suggest that most species of chewing herbivores in tropical forests are limited to feeding on a few closely

related species of host plants. Several comparative studies have suggested, however, that tropical insects may have broader diets than do their temperate counterparts. Dixon *et al.* (1987) showed that polyphagy is a more common habit among aphids (Aphididae) in tropical forests than in temperate ones. Wood & Olmstead (1984) reported that 46% of the treehopper species (Membracidae) in Costa Rica are polyphagous compared with only 16% in Ohio. In a study of wood-feeding beetles (Scolytidae and Platypodidae), Beaver (1979) found that diets were narrower in temperate regions than in the tropics. Beaver argued that these beetles are more generalized in the tropics because their hosts, fallen trees, are not predictable and decay more quickly.

Combined with Marquis's (1991) assessments of the host-specificity of geometrids and weevils on *Piper*, Beaver's comments suggest that the generalist habit may be more common for herbivores that have difficulty in locating suitable hosts, either because of poor dispersal ability or because the hosts themselves are unpredictable (Dixon *et al.* 1987; Coley & Barone 1996). Thus, in diverse tropical forests, chewing herbivores, particularly beetles and moths with good dispersal abilities, may tend to have very narrow diets, whereas smaller, poorly dispersing herbivores may be more likely to have a generalized habit.

BIASES IN DETERMINING DIET BREADTH

Determinations of host-specificity from feeding trials can lead to either under- or over-estimates of diet range. In the present study, under-estimations could have occurred because the feeding trials were limited to using plant species available on BCI. Nine of the 12 species-specialized herbivores were from host

plants that did not have congeners in the forest on BCI. Had congeners been available, I suspect that some of these herbivores would have shown broader diets. Fox & Morrow (1981), however, have argued that the host-specificity of an herbivore should be considered within the context of the local plant community. Therefore, from the perspective of their host plants, these herbivores have very narrow diets.

Another bias could have occurred if the herbivores used in this study were unusually specialized compared with others on BCI because most feed on tree species that are relatively abundant. Most tree species in tropical forests are rare (Hubbell & Foster 1986) and may be difficult for herbivores to locate. As noted above, under such circumstances, their herbivore faunas will be selected to have a broader diet (Beaver 1979; Basset 1992). Because the herbivores in this study come from locally common species, and presumably have less difficulty finding suitable host plants, they may be more specialized than most herbivores in the forest. Thus, extrapolating from this sample to the forest as a whole may be unwarranted.

On the other hand, the feeding trials may also have over-estimated the diets of the herbivores examined, because they simply determined whether herbivores were willing to eat particular plants when no alternative was available. That a hungry herbivore found a plant palatable in a brief trial does not mean necessarily that it could survive and grow on the plant over the long term. Moreover, simply because an herbivore is willing to eat a plant in the laboratory does not indicate that it would ever use the plant in nature. For example, in this study, three herbivore species collected on *H. americana* were able to eat *H. triandra* in feeding trials, but only two of these were ever collected from *H. triandra* (Table 3). Therefore, feeding trials such as these may over-estimate the diet breadths of herbivores.

The method of sampling herbivores in the forest can also bias a study toward finding generalists. As noted above, Basset (1992) reported on a comprehensive census of the herbivore species attacking the tree *A. actinophyllum* in a subtropical forest in Queensland, Australia. He found that 89% of the herbivores had extremely broad diets, feeding from multiple plant families. These determinations were made in part on the basis of feeding trials (which were not described in detail), published records and field observations. He attributed the high proportion of generalists on this tree species to a lack of qualitative defences (e.g. alkaloids) and the low nutrient content of the leaves.

Like this study, Basset's assessment of herbivore specificity was from the perspective of the plant and based on a lengthy period of collection. One hazard of this method was encountered in this study: the number of specialists that were found asymptotes more quickly than does the number of generalists (see Fig. 3). Presumably, this occurs because any given tree

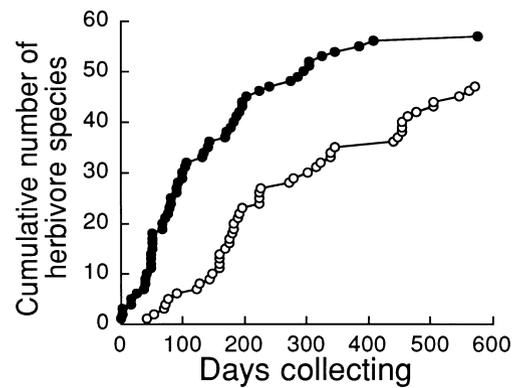


Fig. 3. Cumulative number of herbivore species through time for the final 19 months of the study. Herbivores were collected daily during this period, and each circle represents the first time a new species of herbivore was found. Filled circles represent specialist herbivores (limited to feeding at most on one plant family) and open circles represent generalists (able to eat from more than one plant family). These diet assessments should be considered tentative as they are often based on collections of one or two individuals.

species is not necessarily a preferred host plant for most generalist herbivores, so they only appear in collections in a haphazard fashion. In Basset's (1992) study, the thoroughness of his sampling likely resulted in a complete list of the specialist herbivores for *A. actinophyllum*, but he probably sampled a large proportion of the generalists in that forest as well, thus lowering his estimate of the degree of host specificity. Were another tree species in the same forest sampled, a second group of specialists would be found, as would many of the same generalist species, thus decreasing the overall proportion of generalists. Because of this sampling problem, estimating the degree of host-specificity in a forest from a single tree species seems prone to inaccuracy and Basset's estimates of generalists are probably inflated.

Though I encountered the same sampling problem in this study, two differences should be noted. First, I am reporting results for common chewing herbivore species on the focal tree species used in this study. I am limited to this because of the need for enough individuals to conduct adequate feeding trials. Secondly, by sampling from numerous tree species, my estimates of the proportion of generalists should more closely approximate that in the forest as a whole, especially since many of the generalists were found on more than one tree species. In general, estimates of the proportion of generalists in a study should decline as more tree species are sampled.

YOUNG LEAF HERBIVORES

Both the relative vulnerability of young leaves to herbivores, as well as the preference of many herbivores for young leaves have been well-documented (e.g. Feeny 1970; Lowman 1985; Basset 1991; Aide 1993;

Coley & Kursar 1996). In her work on BCI, Coley (1983) attributed the high rates of damage to young leaves largely to their greater softness and higher nutrient content compared to mature leaves. In this study, the relatively large proportion of herbivores that were limited to feeding on young leaves (24%) may reflect the deterrence of toughness in mature leaves. Two observations reinforce this view. First, three species of the caterpillars that were limited to young leaves in their early instars could feed on the mature leaves in the final instar. Secondly, other species of caterpillars that could feed on mature leaves in early instars shifted their pattern of feeding as they grew, with early instars scraping the leaves and later instars chewing them. This implies that early instar caterpillars cannot muster enough force to chew the tough mature leaves (Bernays & Janzen 1988).

These observations suggest that the proportion of young leaf specialists may differ across tropical forests of different types, depending on the palatability of the mature leaves. Leaves in tropical dry forests typically live for less than a year, whereas those in wet and rain forests frequently last for more than 2 years (Coley & Aide 1991). Plant defence theories predict that longer-lived leaves should be better defended than short-lived leaves, and thus, mature leaves in wetter forests should have traits that make them less palatable to insect herbivores (Grime 1977; Coley, Bryant & Chapin 1985). In a review, Coley & Aide (1991) found that this was, indeed, the case, with mature leaves from shade-tolerant plants in wet tropical forests having greater levels of toughness, lower water contents and lower nitrogen concentrations than those from dry forests. Such differences may be reflected in the feeding habits of herbivores. In contrast to this study, where 24% of the herbivores specialize on young leaves, in Santa Rosa National Park, a dry forest in Costa Rica, very few species of herbivores are thought to specialize on young leaves (D. Janzen, personal communication).

HERBIVORY AND PATHOGEN DAMAGE

At least for young leaves, the herbivory results clearly show that chewing herbivores with narrower diets typically did far more damage than did generalists. Although I believe this may be typical for tropical forests, I am unaware of any comparable data. Fungal pathogens also caused a large amount of damage to the leaves of some species. As can be seen by comparing the results for *Protium tenuifolium* Engler ssp. *sessiliflorum* and *P. panamense* (Rose) I. M. Johnston (Fig. 2), the amount of pathogen damage could differ considerably between related species. This implies that the pathogens may be quite host-specific, but another possibility, that necrosis caused by pathogen infection may manifest itself more slowly on some species, cannot be ruled out.

Though leaf pathogens have received relatively little

attention in tropical forests (Coley & Barone 1996), they have been shown to do considerable damage. Gilbert (1995) measured the amount of pathogen damage to mature leaves in the canopies of five tree species in a dry forest in Panama and found that depending on the species 5–60% of the shade leaves showed signs of fungal infection. Garcia-Guzman & Dirzo (1991) found pathogen damage on 45% of the understorey leaves (from 67 species) and 60% of the canopy leaves (from 30 species) in Los Tuxtlas, Mexico. J. A. Barone (unpublished) showed that damage from pathogens was also greater in the canopy than understorey for two tree species on BCI.

HOST-SPECIFICITY AND DIVERSITY

The relatively high specificity of chewing herbivores reported in this study supports the supposition that each species or genus of tropical tree harbours a unique contingent of herbivore species. This is the essential assumption of Erwin's (1982) calculation of global species diversity and has received support from a variety of fogging studies as well (reviewed in Erwin 1995). Nonetheless, several issues deserve more attention. Marquis's (1991) argument that the dispersal ability of herbivores influences their host-specificity requires investigation. In addition, the biogeography of the tropical herbivores has received little attention, but is necessary in determining whether a tree species has the same complement of herbivores across its entire range. For example, I have seen many of the tree species in this study at other sites in Panama, and they appear to suffer the same kinds of leaf damage, suggesting they always have the same suite of herbivore species. Whether this is true on a broader, regional scale remains to be determined.

Specialist herbivores did far more damage to young leaves than did generalists. Though this finding needs to be replicated at other sites, if generally true, it strongly supports the Janzen–Connell model (Janzen 1970; Connell 1971). The large proportion of genus and family specialists does suggest, however, that the population dynamics envisioned by Janzen and Connell for a single species may really apply to these higher taxonomic groups. In other words, the damage and mortality rate of young trees may be related to their proximity to members of the same genus or family, as well as to their distance to the nearest conspecific.

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