

HERBIVORY AND PLANT DEFENSES IN TROPICAL FORESTS

P. D. Coley and J. A. Barone

Department of Biology, University of Utah, Salt Lake City, Utah 84112

KEY WORDS: herbivory, tropical forests, plant defenses, pathogens, tree diversity, leaf phenology

ABSTRACT

In this review, we discuss the ecological and evolutionary consequences of plant-herbivore interactions in tropical forests. We note first that herbivory rates are higher in tropical forests than in temperate ones and that, in contrast to leaves in temperate forests, most of the damage to tropical leaves occurs when they are young and expanding. Leaves in dry tropical forests also suffer higher rates of damage than in wet forests, and damage is greater in the understory than in the canopy. Insect herbivores, which typically have a narrow host range in the tropics, cause most of the damage to leaves and have selected for a wide variety of chemical, developmental, and phenological defenses in plants. Pathogens are less studied but cause considerable damage and, along with insect herbivores, may contribute to the maintenance of tree diversity. Folivorous mammals do less damage than insects or pathogens but have evolved to cope with the high levels of plant defenses. Leaves in tropical forests are defended by having low nutritional quality, greater toughness, and a wide variety of secondary metabolites, many of which are more common in tropical than temperate forests. Tannins, toughness, and low nutritional quality lengthen insect developmental times, making them more vulnerable to predators and parasitoids. The widespread occurrence of these defenses suggests that natural enemies are key participants in plant defenses and may have influenced the evolution of these traits. To escape damage, leaves may expand rapidly, be flushed synchronously, or be produced during the dry season when herbivores are rare. One strategy virtually limited to tropical forests is for plants to flush leaves but delay "greening" them until the leaves are mature. Many of these defensive traits are correlated within species, due to physiological constraints and tradeoffs. In general, shade-tolerant species invest more in defenses than do gap-requiring ones, and species with long-lived leaves are better defended than those with short-lived leaves.

INTRODUCTION

In tropical forests the evolutionary relationships between herbivores and plants have resulted in an impressive variety of adaptations and interactions. Herbivore pressure has led to the evolution of chemical, mechanical, and phenological defenses in plants. Herbivores in turn have evolved to cope with food plants that are trying to starve or poison them. These relationships affect food webs, nutrient cycling, and community diversity, and thus every organism in tropical forests. In this review we examine the ecological and evolutionary outcomes of the interactions between herbivores and their host plants in lowland tropical rain forests. We begin by summarizing the patterns of herbivory in tropical forests, then turn to the herbivores, their diet breadth, and their strategies for dealing with plant defenses. Next we describe the ecological impact of herbivores and pathogens on the structure and diversity of tropical forests. We conclude with an examination of the wide array of plant defenses against herbivores. Throughout this review, we use the term “herbivory” to refer to leaf damage by insects, mammals, and pathogens. We have chosen this broad definition because all three groups have a profound effect on tropical plant ecology. While most research has focused on insect herbivores, we hope that this wider perspective will encourage more work on mammalian herbivores and, especially, pathogens. Our definition also reflects the practical problem that it is often difficult to distinguish the cause of damage to a leaf. This should be kept in mind in our discussion below of levels of herbivory in tropical forests.

RATES OF HERBIVORY

In this section we review the patterns of herbivory that have been documented in a number of tropical forests. Unfortunately, levels of leaf consumption have been measured in a variety of ways, making comparisons difficult. Nonetheless, we can identify several general results. Most importantly, herbivory in tropical forests is quantitatively and qualitatively different from that in the temperate zone. Moreover, within the tropics rainfall regimes, leaf age, and location in the canopy all influence damage rates.

Temperate vs Tropical Forests

Annual rates of leaf damage are higher in tropical forests than in temperate broad-leaved forests (Table 1). Herbivory averages 7.1% per yr in the temperate zone, and 11.1% for shade-tolerant species in the humid tropics ($p < 0.01$, based on 42 studies). Rates of damage to gap specialists are even higher (48.0%), but they comprise less than 15% of the individual trees in tropical forests (107). Although this latitudinal difference is statistically significant,

Table 1 Comparison of rates of herbivory in temperate and tropical forests.

	Annual		Mature Lves		Young Lves		Young/total	
	%	N	%/d	n	%/d	n	%	n
Temperate	7.1	13					27.0	
Tropical wet forest								
Shade-tolerant species	11.1	21	.03	105	.71	150	68.3	31
Gap specialists	48.0	4	.18	37	.65	37	47.3	30
Tropical dry forest	14.2	4	.07	78	.15	61	28.7	62

Annual is the average percentage damage per year, with N being the number of studies (each study included many species). Daily rates of herbivory are presented for young and mature leaves (%/d), young/total indicates the percentage of the total lifetime damage that occurs while leaves are expanding, n indicates the number of species. Data on young/total from the temperate zone are the average for an entire forest. (3, 5, 23, 30, 31, 47, 60, 62, 65, 78, 97, 118, 132, 137, 140, 144, 147, 160, 161, 163, 181, 182, 190)

it is not enormous, and given the paucity of accurate measures, it should be regarded as a working hypothesis. Moreover, when we discuss forest averages in herbivory, we are ignoring enormous temporal and spatial variation as well as consistent differences among species.

The tropics incur higher rates of damage despite the fact that tropical plants tend to be better defended (see below). This suggests that the high damage rates in the tropics must be due to greater pressure from herbivores, though few studies have attempted to measure the biomass of herbivores in different forests (131).

Assuming these latitudinal trends in herbivory are real, are they important ecologically? Although an annual leaf loss of 10% may not seem extreme, it is sufficient to reduce plant fitness (68). For example, Marquis found that 10% experimental defoliation of an understory shrub, *Piper arieianum*, reduced growth and seed production, delayed flowering, and decreased seed viability (144, 146). Annual survivorship is 85% for undamaged seedlings of *Dipteryx panamensis* and 0% for seedlings with 8% of their leaf area missing (38). Furthermore, most plants allocate only 10% of their resources to reproduction, an investment that obviously affects fitness (18). Hence, herbivory probably has a substantial impact on growth and survival of plants, and more so in the tropics than in the temperate zone.

Wet vs Dry Tropical Forests

Within the tropics, rainfall regimes influence the duration of the dry season. At sites with extended dry seasons, most or all of the tree species become deciduous for portions of each year, whereas in wetter sites, species are evergreen.

Herbivory differs significantly along this rainfall gradient. Dry forest species suffer higher rates of herbivory (14.2%/yr) than do shade-tolerant wet forest species (11.1%/yr) ($p < 0.05$; Table 1). These patterns result in part from the lower levels of defense in short-lived deciduous leaves (47), and in part from the fact that dry seasons reduce herbivore populations (45).

Young vs Mature Leaves

The most striking difference in patterns of herbivory within tropical forests is between mature leaves and young, expanding leaves. Due to the higher nutritional quality of young leaves, daily rates of damage are 5–25 times higher than on mature leaves (Table 1). Despite the fact that leaves are only expanding for a short 1–3 week period, the high rates of damage are significant over the lifetime of a leaf. For tropical shade-tolerant species, whose leaves last an average of 2–4 yr (43, 139), 68% of the lifetime damage occurs during the small window of leaf expansion (Table 1). This is in marked contrast to the temperate zone where only 27% of the lifetime damage accumulates while the leaf is expanding (Table 1). Young temperate leaves may partially escape damage by emerging in early spring when herbivore populations are reduced. Hence, for temperate species, most of the damage occurs on mature leaves, whereas for tropical species the majority of damage accrues while the leaf is young. Although the importance of young leaf herbivory is most pronounced for shade-tolerant species of wet forests, the pattern holds across the tropics and may be the most fundamental difference between temperate and tropical forests. The high absolute and relative rates of herbivory on young tropical leaves suggest that they have experienced stronger selection for defenses. Furthermore, because tropical herbivores depend on such an ephemeral food source, this may select for more elaborate host-finding mechanisms and tighter coupling between herbivore life-history traits and plant phenologies.

Canopy vs Understory Leaves

Recent innovations have led to easier and more reliable access to the tropical forest canopy and increased attention to herbivory on canopy leaves (See Lowman, this volume). In her pioneering work, Lowman examined herbivory on five tree species in subtropical and temperate rain forests in New South Wales, Australia, and found that leaves in the sun usually suffered significantly less damage than shade leaves and that herbivory was higher in the understory than in the canopy (138). Other work in Panama suggests a similar pattern, with lower damage from insect herbivores in the canopy, though pathogen damage may be greater there (15, 93).

Differences in plant chemistry, local microclimate, or predation rates on leaf herbivores have been suggested as possible causes for the decrease in herbivory

with height in forests. Sun leaves are smaller, tougher, and have higher phenolic contents than do shade leaves (96, 138, 141). The canopy typically has a hotter, drier, and windier microclimate as well, which may severely affect many insect herbivores (138). Predation, such as by birds, may also reduce insect herbivore abundances in the canopy relative to the understory. Recent work in Puerto Rico showed that anolis lizards are important predators of insect herbivores in the canopy, thus reducing damage to canopy leaves, but whether their impact is greater in the canopy than in the understory is not known (67).

These three hypotheses concerning the effects of plant chemistry, microclimate, and predation are not mutually exclusive, and their impact may vary with the size and guild of the herbivores in question. In addition, the trend of greater herbivory in the understory suggests that many plant defenses, especially leaf phenology and greening (see below), may be the consequence of selection by herbivores in the understory and that the presence of these traits in adult trees may be holdovers from this earlier life stage.

Methods of Measuring Herbivory

Generalizations about herbivory are difficult, as many of the studies summarized above (Table 1) reported a one-time estimate of standing crop damage. Quantifying the amount of leaf tissue eaten with a single measure of missing leaf area is misleading. First, completely eaten leaves are not included in the sample, so the amount of damage is underestimated. In studies that have compared single measurements to rates derived from repeated measurements of marked leaves, underestimates averaged 50% (from 38–60% ; 39, 78, 137). Second, as leaf longevity differs among species, it is impossible to know the time scale over which damage has accumulated. Across tropical trees, leaves can live from 4 mo to over 14 yr (PD Coley, unpublished data; 43, 176). If these differences are not taken into account, it will be erroneously concluded that species with short-lived leaves have lower damage rates (161). Therefore, a single measure of standing crop damage cannot easily be translated into an annual rate of damage, nor can it be used meaningfully to compare herbivory on different species. Instead, we suggest that investigators measure marked leaves or expanding buds at two different times to calculate a rate of damage, and that they include both expanding and mature leaves in the study.

HERBIVORES

Leaves are subject to damage by an enormously diverse set of vertebrate and invertebrate herbivores as well as by pathogens. Studies document defoliation by all these enemies, but are they equally important? In this section we examine characteristics of each group and discuss how their seasonal and spatial

distributions as well as the degree of diet specialization may influence patterns of herbivory.

Insects

TOTAL CONSUMPTION Folivorous insects are diverse taxonomically and physically, and they are the most important consumers in tropical forests. For example, there are at least 171 phytophagous insect families at La Selva, Costa Rica (147), and 95 different species feed on a single species of understory shrub (145). Although the biomass of vertebrate herbivores in a forest may be twice as high as for insects, insects cause most of the herbivory. On Barro Colorado Island (BCI) in Panama, 72% of the annual leaf consumption, or 575 kg/ha/yr, is eaten by chewing insects (131). The proportion of damage caused by insects may be even higher in other forests. For example, in Parque Nacional Manu, in Peru, arboreal vertebrate folivores are rarer, and together they consume about one sixth as much as their counterparts on BCI (131). So it is not unreasonable to suggest that chewing insects contribute 75% or more to the annual leaf consumption.

Not all herbivores leave obvious evidence of their consumption. The impact of leaf chewers has been best studied because the story can be partially read from the holes in leaves. Phloem feeders are numerically common, yet it is difficult to assess their impact on plant productivity. In a temperate hardwood forest, phloem feeders comprised 23% of the phytophage biomass (181). In Brunei, sucking insects in canopy crowns were as abundant numerically as chewing insects (191), and in a tropical eucalyptus forest, 79% of all herbivores were phloem feeders (77). Although phloem feeders tend to be smaller in body size, they appear to consume more per gram of body mass than chewers (181). Leigh (131) therefore suggested that phloem feeders may remove as much biomass as leaf chewers. Clearly this issue needs a great deal more attention.

SEASONALITY The extent of seasonality in insect numbers reflects the seasonality of rainfall in different forests (147, 205). In general, insect populations are depressed during the dry seasons, with a marked rebound at the beginning of the wet season followed by a gradual increase until the onset of the following dry season (116, 138, 147, 158, 205). Rates of herbivory mirror this pattern, being lowest in the dry season and highest in the rainy season.

DIET SPECIALIZATION OF INSECT HERBIVORES The ecological circumstances and evolutionary pressures that lead to narrow diet breadth in insect herbivores have received considerable attention (71, 88, 108). The topic is particularly important in tropical ecology because many explanations of the high species diversity in tropical forests assert that organisms in the tropics have smaller niche sizes, meaning that more can be packed together in a habitat (142, 143).

For insect herbivores, niche size is directly dependent on diet breadth, making information on host-range critical to understanding the processes that lead to high diversity. In addition, recent projections of both tropical and global species richness have relied on largely untested assumptions of the extent of host-specialization in tropical forests (74, 91). Finally, understanding the degree of host-specialization is critical to evaluating the Janzen-Connell model of tropical forest tree diversity, which assumes that herbivores are specialized (see below; 54, 109).

Two general factors are thought to favor specialization in herbivorous insects—plant defenses and natural enemies. Plant defenses, particularly chemical defenses, require energy to disarm or detoxify. Specialist herbivores should be more efficient in dealing with the defenses of their host plants and thus grow and reproduce more quickly than generalists (71, 95, 113, 128). Natural enemies may also select for a narrow diet breadth in herbivores, if they are better able to locate their prey on some plant species (or plant parts) than others. This differential predation pressure would favor those individual herbivores with a preference for host species where they suffered the lowest mortality, leading to a narrower diet breadth (27, 172).

Both plant defenses and natural enemies may be stronger selective agents in tropical forests, leading to greater specialization than in temperate regions. Plants in tropical forests tend to be better defended chemically than their temperate counterparts (47), and the high diversity of plant species means that herbivores confront a greater array of defenses (113, 116). Conversely, the relative rarity of most plant species in tropical forests means that locating them is more difficult and costly for herbivores, both in terms of time and exposure to predators. Under these circumstances, selection would favor a more generalized habit (16, 20, 108, 113). This should be particularly true for smaller insects, which may be less efficient at locating hosts because of poorer dispersal abilities (144).

PATTERNS OF SPECIALIZATION The common assumption that insect herbivores are more specialized in tropical regions has been tested by relatively few studies (170, 171). Scriber (185) surveyed the global patterns of feeding specialization of the Papilionidae (Lepidoptera) and determined that generalists represent a higher proportion of species at temperate latitudes. Similar patterns hold for other insect groups. Butterflies from three families (Papilionidae, Pieridae, and Nymphalidae) typically have a narrower host range in the wet forest at La Selva, Costa Rica, than they do at five temperate sites (147). The percentage of specialist grasshoppers (Acrididae) is also higher at La Selva than at sites in Texas and Colorado (147). Basset (17) showed in feeding trials that tropical herbivores have a narrower diet than temperate ones, perhaps reflecting greater palatability of temperate trees. Within the tropics many groups show high levels

of specialization (91, 145). *Ithomiine* and *Heliconius* butterflies (Nymphalidae) average between one and three host species (24, 32, 70). Most herbivorous bugs (Hemiptera) from Dumonga Bone National Park in Indonesia are restricted to a single host family (102).

Several studies have provided counterexamples to this level of specialization, however. Treehoppers (Membracidae) show greater host-specificity at higher latitudes (207), as do two families of wood-feeding beetles (Scolytidae and Platypodidae) (20). These beetles feed on fallen trees and branches, which are an unpredictable resource and decay rapidly in the warm, humid climate, making specialization difficult (20). In a study of the herbivores on a single species of tree, *Argyrodendron actinophyllum* (Sterculiaceae) in a subtropical forest in Australia, Basset (16) found that only 11% (of 156 folivorous species) were specialized, feeding on hosts from one or a few related host families. Despite the conclusions of these studies, most herbivorous insects in the tropics appear to be quite specialized, though this question requires more attention (145, 147). Since, in general, most insect herbivore species have narrow host ranges (26), it is difficult to assess whether tropical herbivores are more specialized than temperate ones. We suspect that, both for small herbivores that disperse poorly, such as treehoppers, and for those that feed on unpredictable resources, the problems of host location in diverse tropical forests may overwhelm the selective advantages of specialization, leading to broader diets in tropical forests. Mobile herbivores, such as many beetle species and most moths and butterflies, are probably more specialized than temperate species.

HERBIVORY AND SPECIALIZATION Little is known about the relative proportion of damage caused by specialist and generalist herbivores in tropical forests, yet such information is important to understanding the nature of the selection on plant defenses and how herbivores regulate plant populations. On BCI, about 60% of leaf damage in 9 tree species was due to specialist insect herbivores (feeding on plants in only one plant family), and 8% was from generalists, with the balance from fungal pathogens (JA Barone, unpublished data). The tree species showed considerable variation, but specialist herbivores always caused more damage than generalists. If this pattern of damage holds, it suggests that specialist insect herbivores are more important than generalists in ongoing selection for plant defenses. In addition, it supports the assumption of the Janzen-Connell model (54, 109) that host-specialists do most of the damage to plants in the tropics (see below).

Mammals

ABUNDANCE Although annual net production of vegetation is high in tropical forests and may exceed that of savannas, most of it is in the canopy, out of reach

of terrestrial animals. Densities of terrestrial folivores such as deer and tapir vary significantly among lowland rain forest sites, but average 300 kg km^{-2} (28, 79, 131, 192), which is only 5% of the biomass typical for savannas (119). In rain forests, most of the folivores are arboreal, with a biomass 1.5 to 5 times as high as that of the terrestrial folivores (131). However, even considering both terrestrial and arboreal biomass of folivores, tropical forests have much lower mammalian densities than do savannas. This is because leaves are in the canopy, and there are difficulties associated with arboreality.

CONSTRAINTS ON ARBOREALITY The upper limit on body size for folivorous arboreal mammals is generally considered to be 13–15 kg (72), because size limits the ability to reach leaves at the ends of branches. However, small body size makes digestion of high-fiber and low-nutrient diets more difficult to the extent that animals less than 1 kg may be unable to survive on a strictly folivorous diet (58). Smaller animals need more energy per gram of body weight (122), but the digestive capacity and hence the ability to obtain energy is directly proportional to body size (63). Thus smaller animals have a higher mass-specific energetic demand that must be met by a proportionally smaller energetic input (58). Because of the low nutritional quality of leaves as compared to seeds or animal tissue, there is a limit for the body size of mammalian folivores below which they cannot obtain sufficient energy. The smallest body sizes of folivorous arboreal mammals are less than in terrestrial folivores, suggesting that arboreal mammals may be living closer to the metabolic limits imposed by digestion (58, 152). Because of the poor nutritional quality of mature leaves, many mammals supplement their diets with fruit or seeds, and even strict folivores consume the more nutritious young leaves when possible. On BCI, sloth mortality is highest in the late rainy season, when young leaves are rare, and when extended periods of cooler, rainy weather slow digestion (85, 86; PD Coley, personal observation). In years with late rainy season fruit failure, famine in herbivorous mammals is widespread (85, 86, 153). Terborgh & van Schaik hypothesized that in the Neotropics, seasonal shortages of fruit and new leaves coincide, and that this bottleneck in resource availability may explain the low biomass of primates in South America relative to Africa (194).

DIGESTIVE PHYSIOLOGY Folivores are confronted with a diet that is simultaneously poor in nutritional content and rich in defensive chemicals. A common solution has been to rely heavily on microbial symbionts to ferment the vegetation (200). Mammalian herbivores can be classified as hindgut (e.g. horses) or foregut (e.g. ruminants) fermenters, depending on whether the primary site of fermentation occurs before or after food passes through the stomach. Foregut fermentation is thought to be more efficient at digestion of high

fiber/low nutrient diets, due to longer gut retention times and sieves that allow passage of digested material and retention of fiber in the foregut for continued fermentation (178). In addition, microbes in the foregut may aid detoxification of plant secondary metabolites (61). However, foregut fermentation of only leaves would not provide enough energy to small folivores because passage times are necessarily shorter in animals with small body size (58, 63). Instead, in arboreal herbivores, foregut fermentation is associated with a mixed diet of leaves and seeds or fruits. Nutritionally rich items can pass quickly through the digestive system, while more fibrous material is retained for further microbial fermentation. The one exception, sloths, have unusually low metabolic rates (159) that may allow them, with foregut fermentation, to survive on leaves.

Most arboreal folivores appear to be hindgut fermenters with an added ability for colonic separation (58). Separation of digesta in the cecum-colon allows retention of the nutritious parts of the digesta and rapid excretion of the larger, less digestible particles (80). Cork & Foley (58) suggested that selection for different digestive strategies results primarily from nutritional factors including high fiber and phenolic contents. The interplay between digestion and plant secondary metabolites is as yet unresolved.

Pathogens

Leaf pathogens, a taxonomically diverse and ecologically important group, have not received the research attention they deserve. Nonetheless, damage by these pathogens is common and widespread. In the lowland wet forest of Los Tuxlas, Mexico, Garcia-Guzman & Dirzo (90) found pathogen damage on 45% of the 67 understory species and 60% of the 30 canopy species surveyed. For 25 species on BCI, pathogens accounted for 29% of the damage for which culprits could be identified (PD Coley, TA Kursar, unpublished data). In the canopy of a seasonal dry forest in Panama, 5 kinds of pathogen damage were found on *Anacardium* leaves, and 75% of the *Luehea* leaves were diseased (93). For the tree *Quararibea* on BCI, pathogen damage accounted for 61% of the lost leaf area in the canopy, compared to 2% in the understory (15). In addition to leaf pathogens, fungi responsible for damping-off can kill large numbers of establishing seedlings (9), and stem cankers can attack and kill saplings (94).

ECOLOGICAL IMPACT OF HERBIVORES

Herbivory can have numerous negative effects on plant fitness by depressing growth and reproduction and by reducing competitive ability. In the following section, we examine the consequences of damage by different classes of herbivores to community composition.

Insects

Janzen (109) and Connell (54) proposed that host-specialized seed predators, herbivores, and pathogens can maintain the high diversity of tree species in tropical forests if they are more likely to damage and kill juvenile trees (seeds, seedlings, and saplings) growing at high densities or close to conspecific adults. Such a pattern could occur if the adult trees serve as reservoirs or cues for natural enemies. This higher rate of mortality near adults means that the chance of successful recruitment is likewise low near adults but increases with distance. This distance dependence results in turn in greater spacing between adults of competitively dominant species and permits more species to coexist (54, 105, 109). Most of the studies that have tested the prediction that levels of damage and mortality are higher near adults or at high densities have focused on seeds and seedlings. Of 36 studies¹, 28 have provided at least weak support for the prediction, with 63% (28 of 45) of the tree species across all the studies showing higher mortality or damage near conspecific adults. This distance-dependence in damage and mortality appears most likely when a single, host-specialized natural enemy is the main cause, though the responsible agent was not determined in most studies.

Although they have received little attention, leaf-chewing and leaf-sucking insects could generate the pattern of mortality predicted by the Janzen-Connell model, if damage rates are higher on young trees near conspecific adults (54). Indeed, unlike damage to seeds or seedlings, herbivore damage to saplings and older size classes could accumulate over many seasons, gradually killing off juvenile plants near conspecific adults. In addition, higher rates of herbivory near adults may reduce the growth of juveniles trees, making them more vulnerable to mortality from other causes such as falling branches or secondary pathogen infection.

Community-level studies have shown that these older size classes of young trees can suffer from distance-dependent mortality. In rain forests in Queensland, Australia, Connell and his coworkers frequently observed decreased growth and higher mortality when a tree's nearest neighbor was a conspecific, though such results were largely limited to small size-classes and to very short distances between individuals (55, 57). Condit, Hubbell & Foster have examined recruitment, growth, and mortality of woody stems on a 50-ha permanent plot on BCI (107). They have found that both proximity to conspecific adults and local conspecific density decreases growth and increases mortality of a few abundant tree species (53, 104). Recruitment into older size classes was also less likely near conspecific adults for 15 of the 80 (19%) woody species

¹References: 6–8, 10, 22, 29, 35, 37, 38, 54, 56, 64, 66, 81–84, 87, 94, 103, 104, 110–112, 115, 117, 120, 121, 129, 130, 183, 193, 196, 198, 204, 208.

they examined, though for most of these species the negative effect disappeared beyond distance of 10 m (51, 52). While the strict criteria used in this analysis probably understate the importance of distance-dependence in this forest (131), their results do demonstrate conclusively that the distance and density dependence predicted by Janzen and Connell can continue past the seedling stage.

Insect herbivores likely play a role in generating these effects. Recent work on BCI showed that saplings of three abundant species near adults suffer higher levels of damage to young leaves than do those farther away, with most of this damage caused by specialist herbivores, as predicted by the Janzen-Connell model (J Barone unpublished data). This distance dependence was only seen when nearby conspecific adults were also flushing young leaves, suggesting that adults were either a source or an attractant of the herbivores. Thus, it appears likely that at least part of the distance and density dependence observed in older size classes of young trees is due to herbivores.

Mammals

The impact of arboreal mammals is difficult to assess experimentally. Mammalian folivory is much less than insect damage and is unlikely to account for more than 20% of the leaf area consumed in tropical forest canopies. Over evolutionary time, selection pressure from insects rather than arboreal mammals seems to have shaped leaf defenses (47, 58). In contrast to arboreal mammals, terrestrial mammals significantly depress survival of seeds and seedlings. Comparisons of neotropical areas with and without mammals have uniformly demonstrated increased seed and seedling survival where mammals are absent (66, 133, 187). Excluding vertebrates in Queensland, Australia, enhanced seedling survivorship and height growth (169). In experimental exclosures at Manu, Peru and BCI, Panama, sapling densities were approximately 20% higher than in open control plots after 2 yr (195), due to both increased recruitment and decreased mortality. In an on-going experimental exclosure on BCI, WP Carson (personal communication) has also found 2.5-fold increases in seedling densities, with particularly dense carpets under the parent tree. A compelling example of the long-term role of large mammals is seen in the comparison of two Mexican forests—Los Tuxlas, which has lost all of its browsing mammals, and Montes Azules, which retains most of the fauna (69). Los Tuxlas has 2.3 times the density of seedlings and saplings, but only one third the diversity, presumably because thinning of seedlings by mammalian herbivores offsets competitive dominance. Mammals also can damage seedlings in a distance-dependent fashion, with four out of five studies showing greater survivorship with increasing distance from the conspecific adult (66, 83, 84, 104, 183). Thus, while having a limited impact in terms of leaf area consumed, mammals may

have dramatic effects on plant communities through their consumption of seeds and seedlings.

Pathogens

Pathogens are responsible for significant amounts of leaf damage and may also have impacts on the genetic and species diversity of host plants. Aylor (11) suggested that many pathogens have more restricted dispersal than insects or mammals. Thus we might expect pathogens to become locally abundant on adult trees or even genetically adapted to hosts (93). If adult trees serve as reservoirs of disease, they would be a source of infectious propagules for the seedlings below (54). Infection can be much more damaging to a small shaded plant with limited resources than to the adult. Two excellent examples consistent with the Janzen–Connell model show that juvenile mortality to damping-off disease (9, 121) and a stem canker (94) is greater close to the parent tree. A second consequence of adults serving as disease reservoirs is that local adaptation by the pathogen may occur. Limited dispersal and multiple generations could lead to more virulent pathogens better adapted to the parent genotype (93). As a consequence, offspring that are genetically different from the parent would be favored.

PLANT DEFENSES

Are the high rates of herbivory in tropical forests (Table 1) the result of poorly defended leaves? Apparently not. Leaves of tropical forests have both higher overall levels of defense and a greater diversity of defenses compared to their temperate counterparts (47). We suggest that, in part, this greater commitment to defense is an evolutionary response to elevated pressure from herbivores. In addition, mature leaves in evergreen tropical rain forests are extremely long-lived and must therefore be resistant to both abiotic and biotic damage. Average leaf lifetime for understory plants in tropical lowland rain forests is 3 yr with extremes of 14 yr (47, 139). So the combination of higher rates of herbivory and longer leaf lifetimes would select for higher defense in tropical leaves. Even more striking than the latitudinal patterns for mature leaf defenses are those for young expanding leaves. In the tropics almost 70% of a leaf's lifetime damage occurs while it is expanding (Table 1), suggesting that selection for young leaf defenses should be intense. Below we show that young tropical leaves have abundant and novel defenses, which in many cases, surpass levels seen in mature leaves. The opposite pattern occurs in the temperate zone, where young leaves tend to be less well defended than mature leaves.

Nutritional Quality

Nutritional content of leaves varies among species and across leaf ages. Protein, water, and fiber content may result from abiotic selection for different photosynthetic capabilities or protection from physical damage. However, nutritional content has consequences for herbivory and may also be partially shaped by selection from herbivores and pathogens (157). Low nitrogen and water contents have been repeatedly associated with reduced preference and performance of insects (189). Mature leaves of shade-tolerant tropical species have significantly lower nitrogen and water contents than do temperate leaves (47). Young leaves are almost uniformly higher in nitrogen and water than mature leaves—an apparently unavoidable consequence of cell growth. As this makes them more attractive to herbivores (189), we might expect selection to eliminate unnecessary nitrogen from the leaf. In a survey of more than 200 species from four lowland rain forests in Africa, SE Asia, and Central America, a significant positive relationship was found between young-leaf nitrogen and the rate of leaf growth during expansion (49). Apparently rapid leaf expansion requires high nitrogen, presumably in important metabolic enzymes. No physiological constraint prohibits high nitrogen in slowly expanding leaves, but since it is not required for slow expansion, selection by herbivores should favor reduced levels. Thus the nitrogen level of young leaves may reflect the balance between growth requirements and palatability to herbivores. Fiber poses digestive and mechanical problems to herbivores. Fiber content and leaf toughness, a frequently used composite measure of fiber, are both highly negatively correlated with herbivory (40, 178). In the tropics mature leaves are twice as tough as mature temperate leaves (47). Young tropical leaves are also significantly tougher than young temperate leaves, though both are less than half as tough as when they mature (47). Thus ontogenetic and latitudinal patterns of toughness are consistent with rates of herbivory. Perhaps because toughness is such an effective defense, young tropical leaves toughen rapidly as soon as they reach full size. Although the expansion period varies across species from about 6 to 60 days, all species toughen in only a few days immediately following cessation of leaf expansion (4, 123). In a study of daily herbivory on four species, rates of herbivory dropped fourfold during the 3–5 day period of leaf toughening (123). We therefore suggest that selection by herbivores may have caused toughening to occur as rapidly and as early as possible.

Rapid Leaf Expansion

Herbivory on young leaves comprises most of the lifetime damage for tropical species, so reducing the expansion period would lower overall damage (149, 168). Rapid leaf expansion should impose severe constraints on host-finding

by specialist herbivores and shorten the period of exposure to generalists. Aide & Londoño (4) showed that the main herbivore specializing on young leaves of *Gustavia superba* (Lethycidaceae), a species with fast expansion, has only a 3-day window in which to successfully oviposit, even though the larvae have exceptionally quick developmental times. Ernest (73) found twice the damage on slow- as on fast-expanding *Pentagonia* (Rubiaceae) leaves.

Pathogens may be even more severely affected than insects by rapid expansion. To colonize the appropriate host species, a specialist pathogen must use an insect vector with similar host preferences, or it must produce sufficiently large numbers of spores that random dispersal by wind or rain will ensure arrival at the target species. Yet in a study of 25 understory species on BCI (50), no correlation was shown between expansion rate and pathogen damage in the field, even though extracts from rapidly expanding leaves were less toxic in laboratory assays. This suggests that pathogens have limited dispersal ability that makes them less capable of colonizing fast-expanders. Thus pathogens may be a key selective factor favoring rapid expansion of young leaves. Expansion rates vary by an order of magnitude among species, with some leaves doubling in size in less than a day, and others needing more than 15 days (49). So, although rapid expansion appears to reduce damage by both herbivores and pathogens, many species have slow expansion and must rely on alternative defenses.

Secondary Metabolites

The diversity and abundance of plant secondary metabolites appear to be greater in tropical than in temperate forests. For example, a survey of the distribution and activity of alkaloids shows that they are more common and more toxic in the tropics (134, 135). About 16% of the temperate species surveyed contain alkaloids as compared to more than 35% of the tropical species (47). Phenolic compounds, as measured by the Folin Denis assay, do not show obvious latitudinal trends. In a literature review of mature leaves of 282 species in temperate, tropical dry, and tropical wet forests, concentrations of phenols average 6.9% dry weight [range, 6.5%–7.4% dry weight (dw)] and do not significantly differ between forest types (47). However, condensed tannins in mature leaves, measured by the BuOH/HCl method, are almost three times higher in the tropical forests ($n = 268$ species, temperate mean = 1.9% dw, tropical mean = 5.5% dw) (21, 47, 197). Tropical leaves contain many other classes of secondary metabolites, but we know of no comparative studies across tropical or temperate communities. Although mature leaves in the tropics appear to invest heavily in secondary metabolites, the young expanding leaves show the most dramatic commitment to chemical defense (49).

Toughness, the most effective defense (4, 40, 127, 141), is not compatible with leaf expansion, so young leaves must rely on other defenses. Although it

was originally suggested that the problems of sequestering secondary metabolites during cell division and expansion would pose insurmountable problems for young leaves (148, 168), that appears not to be the case. In tropical trees, mono-, sesqui-, and diterpenes reach higher concentrations in young as compared to mature leaves (59, 127), and levels of simple phenolics and condensed tannins are almost twice as high ($n = 125$ species) (21, 47, 197). In contrast, young temperate leaves have twice the level of total phenols, but only half the level of condensed tannins as mature leaves ($n = 7$ species; 47).

Young tropical leaves also have high concentrations of anthocyanins, which cause the dramatic red coloration that has captured scientific and casual interest for decades (34, 100, 167). Several investigators have argued that the selective advantage of anthocyanins is to screen harmful UV (129) or to protect against photoinhibition (98). However, since anthocyanins are associated primarily with shade-tolerant plants and are only present during leaf expansion, adaptive explanations relating anthocyanin to light have been questioned (46). Instead, it has been demonstrated that anthocyanins have antifungal properties (46) that may be particularly important during leaf expansion when the cuticle is poorly developed and risk from pathogen attack is high (PD Coley, TA Kursar, unpublished data; 46, 90). Data on other secondary metabolites are spotty, although we suggest they may also be more common in young expanding leaves than in mature leaves. Coley & Kursar (49) suggest that at full expansion, toughness may play a more important role, and investment in chemical defenses can be relaxed. It would therefore be advantageous for expanding leaves to invest in compounds that could easily be reclaimed (149, 150). The most likely candidates for this are low molecular weight compounds such as monoterpenes, toxic proteins and amino acids, cyanogenic compounds, alkaloids, and saponins. Furthermore, if costs are associated with turnover of these compounds (92), it may be too expensive to use them as defense in long-lived mature leaves, but reasonable for defense during expansion (48). For these reasons we expect the diversity and quantity of low molecular weight compounds to be extremely high in young leaves.

Investment in secondary metabolites may be lower in rapidly expanding young leaves because of a greater risk of autotoxicity (149, 177) or because resource input into the leaf may simply not be sufficient for both rapid expansion and synthesis of secondary metabolites (156, 168). This hypothesis is supported by studies showing that shoot tips of chemically well-defended plants elongate more slowly than those of less-protected relatives (168, 174). In general, rapidly expanding young leaves have significantly higher damage rates in the field than do slow expanders (49), apparently due to differences in chemical defense. Extracts from fast-expanding young leaves were preferred by insects in feeding

trials and supported greater fungal growth than extracts from slow-expanders ($n = 25$ species; PD Coley, TA Kursar, unpublished).

Delayed Greening

In many tropical species, young leaves have reduced chlorophyll contents and appear white, pink, or red. Because of the visually dramatic impact of red young leaves, most investigators have focused on understanding the role of anthocyanins (see above). However, more remarkable is the fact that these leaves have altered development such that the normal process of greening is delayed until after full leaf expansion (12, 13, 49). This developmental pattern is extremely common and has apparently arisen independently many times. In a survey of 250 tropical tree species in 44 families, 33% of the species and 61% of the families had delayed greening (49). TA Kursar & PD Coley (195) argue that delayed greening has evolved because it reduces the amount of resources lost for a given amount of herbivory. In delayed greening, chloroplast development is postponed until after the leaf has reached full size, toughened, and is better protected from herbivores (125). As a consequence, young leaves with delayed greening have approximately 10–20% lower levels of light harvesting proteins, photosynthetic enzymes, chlorophyll, and lipid-rich membranes than do normally greening leaves (13, 123, 124). Although ultimately the mature leaves of species with normal and delayed greening have similar photosynthetic characteristics and construction costs, the timing of investment differs (49).

The benefits of delayed greening occur because lower protein and energy contents during expansion translate to a lower loss of resources for a given amount of herbivory (49). The cost is reduced photosynthesis (124, 125). Kursar & Coley compared costs and benefits in habitats with different light regimes to determine if delayed greening was ever cost effective (49, 123–125). Their analysis shows that at the light and herbivory levels typical of tropical forest understories, leaves with delayed greening cost less. However, at the higher light levels of gaps or even temperate forest understories, rates of herbivory would have to be near 100% to balance the increased cost of forfeited photosynthesis. Thus, the analysis suggests that the understory of tropical forests is the only habitat where light is sufficiently low and herbivory sufficiently high to favor delayed greening. And, in fact, delayed greening is restricted to shade-tolerant tropical species (123). Not all shade-tolerant species delay greening. There is a significant negative correlation between expansion rate and chlorophyll content (49). Delayed greening is therefore most common in species with rapid leaf expansion and low investments in chemical defense. As we argued for secondary metabolites, resource limitation in rapid expanders may make simultaneous investment in growth and greening impossible. Furthermore, delayed

greening would reduce the impact of intense herbivory. Thus both physiological constraints and selection would favor delayed greening in rapid expanders. Slow expanders, which are also better defended chemically, would gain little benefit from delayed greening but would pay the cost over a long period of time. So although delayed greening is physiologically possible in slow expanders, selection would favor normal development.

Leaf Phenology

Another strategy plants in tropical forests may use to avoid herbivory on young leaves is to alter the phenology of leaf production (1, 75, 136, 149). This can be done in two ways. First, leaf production may be shifted to peak during the time of year when herbivore abundance is lowest, which is the dry season in most forests. Second, leaves can be flushed synchronously, saturating herbivores with an abundance of leaves to ensure that some escape damage, an idea analogous to mast fruiting as a way to avoid seed predators (3).

LEAF PRODUCTION WHEN HERBIVORES ARE RARE During times of the year when herbivores are rare in a forest, rates of damage to young leaves are lower. In the Accra dry forest in southeastern Ghana, herbivore damage to young leaves was lowest at the start of the wet season (136). Likewise, in two dry forests in south India, trees that flushed new leaves during the dry season suffered significantly less damage than those that produced new leaves during the wet season (158). This pattern was also found in the moist, semideciduous forest on BCI (1, 3). Aide (2) experimentally demonstrated a seasonal escape from herbivory on BCI using the shrub *Hybanthus prunifolius*, which normally flushes in the dry season when herbivore numbers are low (2). Plants forced to produce new leaves in the wet season suffered significantly more herbivore damage than those that naturally produced leaves in the dry season (2). Nevertheless, it is not clear that a seasonal shift in leaf production to avoid herbivory is a viable strategy for plants in forests with weak or short dry seasons, since the abundances of insect herbivores do not decline dramatically under such conditions (206). Have low rates of herbivory during the dry or early wet season been the determining factor in the timing of leaf production? Three factors, water availability, solar radiation, and herbivory, potentially are critical to the evolution of the timing of leaf production (199). In dry, deciduous forests, present evidence suggests that water stress in the dry season limits leaf production (175, 199, 210). In wetter forests where dry seasons are shorter and water stress is less severe, trees may concentrate leaf production in the sunniest times of the year to avoid light limitation during the rainy season (199, 210), though this hypothesis has been disputed (175). Alternatively, trees in wetter forests may produce leaves in response to individual

and "endogenous" factors, with individual trees within a species behaving independently (175).

This current emphasis on abiotic factors in the evolution of the timing of leaf production does not rule out a role for herbivores, but assessing their influence is difficult, largely because of the coincidence of low herbivore numbers and peak irradiance at the end of the dry season (199, 209). Wright & van Schaik (210) noted that one way to disentangle these factors is to look at leaf production in forests where herbivore abundances are high during the dry season, as occurs in Gabon (101). They found that leaf production peaks when both irradiance and insect abundances are greatest, suggesting that for this forest, herbivores are less important than light levels in determining when leaves are produced (210). More of such comparative studies are needed, however, before the role of herbivores in influencing leaf production can be fairly assessed.

SYNCHRONY OF LEAF FLUSHING Increased synchrony in leaf production may also be an adaptation to avoid herbivory. In Ghana, tree species that were more synchronous were less likely to suffer insect damage to young leaves (136). On BCI, Aide found that for the 10 most self-synchronous species he studied, herbivore damage was significantly higher on leaves produced outside of the peak months of leaf production, suggesting that herbivore pressure is maintaining synchrony in these species (3). He also showed, however, that species producing leaves more or less continuously also suffered lower rates of herbivore damage, presumably by using chemical defenses (3, 49).

If herbivores do play an important role in selecting for synchrony in at least some plant species in tropical forests, then the degree of diet-specialization by herbivores should have an impact on the level of synchrony in the forest. If the most damaging herbivores in a forest are generalists, then selection would favor synchrony at the community level. On the other hand, if most damage is done by herbivores that are specialized to a single species, as seems to be the case, then selection would favor individuals that were synchronous with conspecifics, but there would be no particular advantage (or disadvantage) to flushing simultaneously with any other species.

Compared to herbivores, pathogens have probably had a negligible role in selecting for synchronous leaf production in their host plants. Because insect herbivores actively seek young host leaves, the chance that any particular young host leaf will be discovered decreases with higher numbers of young leaves. This is why leaves produced synchronously have lower damage rates from insects than those produced at other times. But for pathogens dispersed haphazardly through the forest by wind and rain, the chance that any young host leaf will be colonized is independent of the abundance of young host leaves. In other words, insect herbivores can be satiated, but pathogens cannot be. If

anything, synchrony of leaf production may result in higher rates of pathogen damage, if spore release by pathogens coincides with leaf production. Unfortunately, no data are available to test these hypotheses.

Third Trophic Level

Thus far, we have focused largely on the interactions between plants and their herbivores. Yet, as has been recognized for some time, the predators, parasitoids, and pathogens of herbivores greatly influence these interactions, and this is reflected in the defenses employed by plants (see 172 for a review). Here we focus briefly on a few issues as they relate to tropical forests.

The antiherbivore defenses of tropical plants have evolved within the context of a community that includes the natural enemies of their herbivores. For this reason, "quantitative defenses" such as tannins or toughness are effective against herbivores even though they do not present an absolute barrier to herbivores. Instead these defenses slow herbivore growth and lengthen the time that herbivores are exposed to predators and parasitoids (75, 172, 177). As the majority of feeding occurs in the final instars, predation will reduce leaf damage. The high levels of these defenses in mature leaves of tropical plants and the relative rarity of insects that feed on mature leaves (JA Barone, unpublished data) suggest that the plants have consistently relied on the enemies of herbivores throughout their evolution. We believe that tropical forests are "green" in large part because the natural enemies of herbivores make quantitative defenses effective.

Plants have also evolved adaptations to attract ants and use them as a defense (25). The production of ant attractants has been predicted to be more common in plants with short-lived leaves, because a continuous investment is needed to feed the ants, and as a leaf ages this cost eventually exceeds that of investing in quantitative defenses (150). Gap species typically have high rates of leaf turnover (48) and, with readily available light, have an abundance of carbon, which makes sugar and lipid awards relatively cheap (19, 165). In a survey of 243 plant species on BCI, gap species were indeed more likely to have attractants than were understory species (184).

Unlike ants, the defensive role of mites on plants has received little attention. Plants may use mites as "bodyguards" against fungal and bacterial pathogens (201, 202). Domatia, specialized chambers in leaf axils, presumably function to house mites, and these occur in 28% of the world's dicot families. In a survey of North Queensland rain forests, 15% of trees had domatia, and 50% of the domatia contained mites (166). Over 80% of the mites were scavengers or fungivores, with only a few being plant parasites (202). Although this suggests mites may benefit the plant by feeding on fungal spores and thereby reducing infection rates, no studies have tested this idea.

Interactions Among Defensive Characteristics of Young Leaves

The high rates of herbivory on young tropical leaves might suggest that selection should favor investment in a large fraction of the defenses described above. However, each species invests in only a small subset of possible defenses. Furthermore, we consistently see the same suites of co-occurring traits across unrelated species. Convergence on similar combinations of traits suggests tradeoffs or physiological constraints that limit the defensive possibilities. We discussed specifics of these relationships in previous sections, so here we describe only the general patterns.

Common defensive patterns were identified primarily from a survey of more than 200 tropical woody species from four forests in Africa, SE Asia, and Central America (49). Each forest had the same emergent associations of rapid leaf expansion, high nitrogen, delayed greening, low toughness, low secondary metabolites, and synchronous leaf flushing. We suggest that by examining the relationships among traits, we can explain why particular sets of traits co-occur. For example, although high nitrogen makes leaves more palatable, it is required for rapid expansion. Because of resource limitation, it is physiologically impossible simultaneously to expand rapidly, green normally, and synthesize secondary metabolites. Because rapid expanders suffer high rates of herbivory, the added protection of synchrony and delayed greening would be favored by selection. And finally, ant defense is most effective on species with continuous leaf production. Thus, the various defensive traits are connected by physiology or selective advantages such that an individual trait is predictably and somewhat inflexibly tied to the entire suite of defenses.

INTERSPECIFIC PATTERNS OF DEFENSE

We have presented general patterns of defense and have highlighted differences between tropical and temperate systems. However, within the tropics, the variation in both herbivory and defense is enormous, dwarfing the latitudinal differences. In the following section, we discuss several clear interspecific trends in defense.

Leaf Lifetime and Defense

A positive correlation exists between leaf lifetime and the commitment to defenses, presumably because the value to the plant and the risk of discovery both increase with leaf lifetime (75, 149, 177, 188). Most gap-demanding species have leaves that last less than six months and are relatively palatable to herbivores (Table 1; 47, 163). Leaf lifetimes for shade-tolerant species are longer, from 1 to 14 yr, and leaves are better defended (40). Furthermore, even within

shade-tolerant species growing in the same habitat, leaf lifetime is negatively correlated with herbivory and positively correlated with defenses such as tannins and fiber (43, 47). Comparisons of vertebrate herbivory in deciduous and evergreen forests are consistent with increased defense in long-lived leaves. Two deciduous forests in India support 10 times the biomass of large herbivores than do three evergreen forests in Africa and the Neotropics (119). In Madagascar, rainfall is significantly negatively correlated with the biomass of folivorous lemurs; lemur biomass in drier, deciduous forests is eight times higher (89). Similar patterns are seen with colobine monkeys in Africa and Asia (164, 203). Ganzhorn (89) attributes the lower biomass of herbivores in evergreen forests to a relatively higher fiber content in the long-lived leaves.

Light and Nutrients

A common evolutionary response to habitats where light or nutrients are limiting is slow growth and lower rates of leaf turnover (36, 99). For species with slow growth, it is hypothesized that opportunity costs of defense will be lower, and the relative impact of herbivory will be higher, than in faster growing species (48, 99). Furthermore, because more resources have been invested in long-lived leaves and replacement is costly, leaf lifetime should be positively correlated with defense (75, 99, 114, 149, 150, 177). Consistent with these hypotheses is the common observation that species from nutrient poor forests have well-defended leaves (42, 48, 114, 151, but see 197).

Light gaps made by treefalls create a mosaic of high light habitats within a rain forest. Presumably because of their rapid growth and short leaf lifetimes, species that specialize on gaps are poorly defended and as a consequence suffer higher rates of herbivory (Table 1). Gap-specialists have similar concentrations of simple phenols but significantly lower condensed tannin, toughness, and fiber contents as compared to shade-tolerant species (21, 47, 197).

INTRASPECIFIC PHENOTYPIC VARIATION IN DEFENSE

The environment can also strongly modify the phenotypic expression of defenses in a given individual. The carbon/nitrogen balance hypothesis (33) suggests that resources in excess of growth demands are shunted to defenses. Thus, high light should lead to elevated photosynthesis and carbohydrate accumulation, which would cause an increase in carbon-based defenses such as tannins and terpenes. Much evidence from the tropics supports this (41, 65, 76, 126, 154, 162, 179, 180). Because the carbon/nitrogen ratio of tissue is high in the light, nitrogen-based defenses should decrease (33), though adequate tests of this prediction are lacking. The phenotypic response to light is

opposite to the pattern seen across species (18). Selection has favored high levels of carbon-based defenses in shade-tolerant species, yet moving a plant from sun to shade reduces these same defenses. Although this seems to cause confusion, there is no reason to expect phenotypic responses to imbalances in source/sink relationships to follow the same trends as evolved differences among species (44). It is therefore misleading and inappropriate to apply the carbon/nitrogen balance hypothesis to explain interspecific defensive patterns. Furthermore, comparing defense levels of gap specialists in the sun with shade-tolerant species in the shade confounds these opposing phenotypic and genetic trends (14). Comparisons between closely related species with different habitat requirements frequently show patterns more typical of phenotypic responses, e.g. similar or higher levels of phenolic compounds in the sun species (40, 65). We suggest that this results from phylogenetic constraints, as species in the same genus have pathways for secondary metabolism that shared a recent common ancestor. Therefore, although selection may be favoring a downregulation of carbon-based metabolites in the gap species, this may be masked by a phenotypic increase because plants exist in a high light habitat. Thus, defensive patterns displayed by congeners may not be "optimal" for their current habitats, especially when they do not mirror common patterns seen in ecologically similar but unrelated species.

CONCLUSIONS

Overall, tropical forests have been shaped by strong ecological and evolutionary interactions between plants and herbivores. The elevated rates of leaf damage, compared to those of the temperate zone, have apparently selected for a greater investment in a diversity of defenses. Particularly distinctive is the fact that the majority of leaf damage in tropical forests occurs on the young, expanding leaves. Mature leaves commonly have defenses, such as tannins and toughness, that function by slowing the growth of herbivores, making them more vulnerable to predators and parasitoids. Insect herbivores display a high degree of diet specialization in the tropics and are responsible for a majority of the leaf damage.

These conclusions suggest several areas for productive research in the future. First, the high degree of diet specialization by insect herbivores should lead to tight linkages between the population dynamics of herbivores and their hosts. Moreover, as the majority of herbivores depend on young leaves, a well-defended and ephemeral resource, host plants may exert particularly strong selection on herbivore life histories and detoxification abilities. Second, although pathogens may cause a third of the leaf damage in tropical forests and may be as important as insects in determining the success of different host genotypes or species, they have received very little attention. Third,

insect herbivores and pathogens are strongly influenced by differences in the length of the dry season, and thus the strength of their impact may vary with precipitation. Furthermore, because of the generally lower levels of defense in deciduous leaves, mammals may be more common and may make a relatively larger contribution to herbivory in dry forests. Comparative studies between forests with different rainfall regimes would no doubt prove very informative. Finally, what ultimately distinguishes tropical forests from other ecosystems is that their community structure results from long-term and intricate biotic interactions involving plants, their consumers and natural enemies. With the rapid destruction of tropical forests and the threat of global climate change, a greater understanding of the importance of these interactions, and how they are altered by fragmentation, is essential to the preservation of tropical forests.

ACKNOWLEDGMENTS

We are extremely grateful to Thomas A Kursar who helped develop most of the ideas presented here. The manuscript benefited from comments by D Dearing, B Howlett, T Kursar, R Lee, E Leigh, V Sork, S Talley, and S Torti. We appreciate financial support from the National Science Foundation (DEB-9420031 to PDC) and the Smithsonian Tropical Research Institute (to PDC and JAB).

Any *Annual Review* chapter, as well as any article cited in an *Annual Review* chapter, may be purchased from the Annual Reviews Preprints and Reprints service.
1-800-347-8007; 415-259-5017; email: arpr@class.org Visit
the *Annual Reviews* home page at
<http://www.annurev.org>.

Literature Cited

1. Aide TM. 1988. Herbivory as a selective agent on the timing of leaf production in a tropical understory community. *Nature* 336:574-75
2. Aide TM. 1992. Dry season leaf production: an escape from herbivory. *Biotropica* 24:532-37
3. Aide TM. 1993. Patterns of leaf development and herbivory in a tropical understory community. *Ecology* 74:455-66
4. Aide TM, Londoño EC. 1989. The effects of rapid leaf expansion on the growth and survivorship of a lepidopteran herbivore. *Oikos* 55:66-70
5. Aide TM, Zimmerman JK. 1989. Patterns of insect herbivory, growth, and survivorship in juveniles of a neotropical liana, *Connarus turczaninowii* (Connaraceae). *Ecology* 71:1412-21
6. Augspurger CK. 1983. Offspring recruitment around tropical trees: changes in cohort distance with time. *Oikos* 40:198-96
7. Augspurger CK. 1983. Seed dispersal of the tropical tree, *Platydictyon elegans*, and the escape of its seedlings from fungal pathogens. *J. Ecol.* 71:759-71
8. Augspurger CK. 1984. Seedling survival of tropical tree species: interactions of dispersal distance, light-gaps, and pathogens. *Ecology* 65:1705-12
9. Augspurger CK. 1990. The potential impact of fungal pathogens on tropical plant reproductive biology. In *Reproductive Ecology of Tropical Forest Plants*, ed. KS Bawa, M Hadley, pp. 237-45. Paris: Parthenon

10. Augspurger CK, Kitajima K. 1992. Experimental studies of seedling recruitment from contrasting seed distributions. *Ecology* 73:1270–84
11. Aylor DE. 1978. Dispersal in time and space: aerial pathogens. In *Plant Disease: An Advanced Treatise*, ed. JG Horsfall, EB Cowling, pp. 159–80. New York: Academic
12. Baker NR, Hardwick K. 1973. Biochemical and physiological aspects of leaf development in cacao (*Theobroma cacao*). I. Development of chlorophyll and photosynthetic activity. *New Phytol.* 72:1315–24
13. Baker NR, Hardwick K, Jones P. 1975. Biochemical and physiological aspects of leaf development in cacao (*Theobroma cacao*). II. Development of chloroplast ultrastructure and carotenoids. *New Phytol.* 75:513–18
14. Baldwin IT, Schultz JC. 1988. Phylogeny and the patterns of leaf phenolics in gap- and forest-adapted *Piper* and *Miconia* understory shrubs. *Oecologia* 75:105–9
15. Barone JA. 1994. Herbivores and herbivory in the canopy and understory on Barro Colorado Island, Panama. *1st Int. Canopy Conf.*, Selby Bot. Gard., Sarasota, FL. (Abstr.)
16. Basset Y. 1992. Host specificity of arboreal and free-living insect herbivores in rain forests. *Biol. J. Linn. Soc.* 47:115–33
17. Basset Y. 1994. Palatability of tree foliage to chewing insects: a comparison between a temperate and a tropical site. *Acta Oecol.* 15:181–91
18. Bazzaz FA, Chiariello NR, Coley PD, Pitelka LF. 1987. Allocating resources to reproduction and defense. *Bioscience* 37:58–67
19. Beattie AJ. 1985. *The Evolutionary Ecology of Ant-Plant Mutualisms*. Cambridge: Cambridge Univ. Press. 182 pp.
20. Beaver RA. 1979. Host-specificity of temperate and tropical animals. *Science* 281:139–41
21. Becker P. 1981. Potential physical and chemical defenses of *Shorea* seedling leaves against insects. *Malay. For.* 2/3:346–56
22. Becker P, Wong M. 1985. Seed dispersal, seed predation, and juvenile mortality of *Aglaia* sp. (Meliaceae) in lowland Dipterocarp Rainforest. *Biotropica* 17:230–37
23. Benedict F. 1976. *Herbivory rates and leaf properties in four forests in Puerto Rico and Florida*. PhD thesis. Univ. Fla., Gainesville
24. Benson WW. 1978. Resource partitioning in passion vine butterflies. *Evolution* 32:493–518
25. Bentley B. 1977. Extra-floral nectaries and protection by pugnacious bodyguards. *Annu. Rev. Ecol. Syst.* 8:407–27
26. Bernays EA, Chapman RF. 1994. *Host-Plant Selection by Phytophagous Insects*. New York/London: Chapman & Hall. 312 pp.
27. Bernays EA, Graham M. 1988. On the evolution of host specificity in phytophagous arthropods. *Ecology* 69:886–92
28. Bodmer RE. 1989. Ungulate biomass in relation to feeding strategy within Amazonian forests. *Oecologia* 81:547–50
29. Boucher DH. 1981. Seed predation by mammals and forest dominance by *Quercus oleoides*, a tropical lowland oak. *Oecologia* 49:409–14
30. Bray JR. 1961. Measurement of leaf utilization as an index of minimum level of primary consumption. *Oikos* 12:70–74
31. Brown BJ, Ewel JJ. 1987. Herbivory in complex and simple tropical successional ecosystems. *Ecology* 68:108–16
32. Brown KS Jr. 1987. Chemistry at the Solanaceae/Ithomiinae interface. *Ann. Mo. Bot. Gard.* 74:359–97
33. Bryant JP, Chapin FS III, Klein DR. 1983. Carbon/nutrient balance of boreal plants in relation to vertebrate herbivory. *Oikos* 40:357–68
34. Burgess PF. 1969. Colour changes in the forest. *Malay. Nat. J.* 22:171–73
35. Burkey TV. 1994. Tropical tree species diversity: a test of the Janzen-Connell Model. *Oecologia* 97:533–40
36. Chapin FS III. 1980. The mineral nutrition of wild plants. *Annu. Rev. Ecol. Syst.* 11:261–85
37. Clark DA, Clark DB. 1984. Spacing dynamics of a tropical rain forest tree: evaluation of the Janzen-Connell model. *Am. Nat.* 124:769–88
38. Clark DB, Clark DA. 1985. Seedling dynamics of a tropical tree: impacts of herbivory and meristem damage. *Ecology* 66:1884–92
39. Coley PD. 1982. Rates of herbivory on different tropical trees. See Ref. 132, pp. 123–32
40. Coley PD. 1983. Herbivory and defensive characteristics of tree species in a lowland tropical forest. *Ecol. Monogr.* 53:209–33
41. Coley PD. 1986. Costs and benefits of defense by tannins in a neotropical tree. *Oecologia* 70:238–41
42. Coley PD. 1987. Patrones en las defensas de las plantas: ¿ porque los herbivo-

- ros prefieren ciertas especies? *Rev. Biol. Trop.* 35:251–63
43. Coley PD. 1988. Effects of plant growth rate and leaf lifetime on the amount and type of anti-herbivore defense. *Oecologia* 74:531–36
 44. Coley PD. 1993. Gap size and plant defenses. *Trends Ecol. Evol.* 8:1–2
 45. Coley PD. 1996. Effects of climate change on plant-herbivore interactions in moist tropical forests. *Clim. Change.* In press
 46. Coley PD, Aide TM. 1989. Red coloration of tropical young leaves: a possible antifungal defence? *J. Trop. Ecol.* 5:293–300
 47. Coley PD, Aide TM. 1991. A comparison of herbivory and plant defenses in temperate and tropical broad-leaved forests. See Ref. 173, pp. 25–49
 48. Coley PD, Bryant JP, Chapin FS III. 1985. Resource availability and plant anti-herbivore defense. *Science* 230:895–99
 49. Coley PD, Kursar TA. 1996. Anti-herbivore defenses of young tropical leaves: physiological constraints and ecological tradeoffs. See Ref. 186, pp. 305–36
 50. Coley PD, Kursar TA, Fikstad T, Rosen-green L. 1995. Chemical defense against pathogens and herbivores is related to expansion rates of young leaves. *Ecol. Soc. Am.* (Abstr.) 76:
 51. Condit R, Hubbell SP, Foster RB. 1992. Recruitment near conspecific adults and the maintenance of tree and shrub diversity in a neotropical forest. *Am. Nat.* 140:261–86
 52. Condit R, Hubbell SP, Foster RB. 1992. Short-term dynamics of a neotropical forest. *BioScience* 42:822–28
 53. Condit R, Hubbell SP, Foster RB. 1994. Density dependence in two understory tree species in a neotropical forest. *Ecology* 75:671–80
 54. Connell JH. 1971. On the role of natural enemies in preventing competitive exclusion in some marine animals and in rain forest trees. In *Dynamics of Populations, Proceedings of the Advanced Study Institute on Dynamics of Numbers in Populations, Oosterbeek, 1970*, ed. PJ den Boer, GR Gradwell, pp. 298–312. Wageningen, Netherlands: Cent. Agric. Publ. Doc.
 55. Connell JH. 1978. Diversity in tropical rain forests and coral reefs. *Science* 199:1302–10
 56. Connell JH. 1979. Tropical rain forests and coral reefs as open nonequilibrium systems. In *Population Dynamics*, ed. RM Anderson, BD Turner, LR Taylor, pp. 141–61. Oxford/London: Blackwell Sci.
 57. Connell JH, Tracey JG, Webb LJ. 1984. Compensatory recruitment, growth and mortality as factors maintaining rain forest tree diversity. *Ecol. Monogr.* 54:141–64
 58. Cork SJ, Foley WJ. 1991. Digestive and metabolic strategies of arboreal mammalian folivores in relation to chemical defenses in temperate and tropical forests. In *Plant Defenses Against Mammalian Herbivory*, ed. RT Palo, CT Robbins, pp. 133–66. Boca Raton: CRC
 59. Crankshaw DR, Langenheim JH. 1981. Variation in terpenes and phenolics through leaf development in *Hymenaea* and its possible significance to herbivory. *Biochem. Syst. Ecol.* 9:115–24
 60. Crossley DA Jr, Gist CS, Hargrove WW, Ridley LS, Schowalter TD, Seated TR. 1988. Foliage consumption and nutrient dynamics in canopy insects. In *Forest Hydrology and Ecology at Coweeta*, ed. WT Swank, DA Crossley Jr, pp. 193–205. New York: Springer-Verlag
 61. Dasilva GL. 1992. The western black and white colobus as a low-energy strategist: activity budgets, energy expenditure and energy intake. *J. Anim. Ecol.* 61:79–91
 62. de la Cruz M, Dirzo R. 1987. A survey of the standing levels of herbivory in seedlings from a Mexican rain forest. *Biotropica* 19:98–106
 63. Demment MW, Van Soest PJ. 1985. A nutritional explanation for body-size patterns of ruminant and nonruminant herbivores. *Am. Nat.* 125:641–72
 64. Denslow JS. 1980. Notes on the seedling ecology of a large-seeded species of Bombacaceae. *Biotropica* 12:220–21
 65. Denslow JS, Schultz JC, Vitousek PM, Strain BR. 1990. Growth responses of tropical shrubs to treefall gap environments. *Ecology* 71:165–79
 66. DeSteven D, Putz FE. 1984. Impact of mammals on early recruitment of a tropical canopy tree, *Dipteryx panamensis*, in Panama. *Oikos* 43:207–16
 67. Dial R, Roughgarden J. 1995. Experimental removal of insectivores from rain forest canopy: direct and indirect effects. *Ecology* 76:1821–34
 68. Dirzo R. 1984. Herbivory, a phytocentric overview. In *Perspectives in Plant Population Biology*, ed. R Dirzo, J Sarukhan, pp. 141–65. Sunderland, MA: Sinauer
 69. Dirzo R, Miranda A. 1991. Altered patterns of herbivory and diversity in the forest understory: a case study of possible consequences of contemporary defauna-

- tion. See Ref. 173, pp. 273–87
70. Drummond BA III. 1986. Coevolution of Ithomiine butterflies and Solanaceous plants. In *Solanaceae: Biology and Systematics*, ed. WG D'Arcy, pp. 307–27. New York: Columbia Univ. Press
 71. Ehrlich PR, Raven PH. 1964. Butterflies and plants: a study in coevolution. *Evolution* 18:586–608
 72. Eisenberg JF. 1978. The evolution of arboreal folivores in the class Mammalia. In *The Ecology of Arboreal Folivores*, ed. GG Montgomery, pp. 135–52. Washington, DC: Smithsonian Inst.
 73. Ernest KA. 1989. Insect herbivory on a tropical understory tree: effects of leaf age and habitat. *Biotropica* 21:194–99
 74. Erwin TL. 1982. Tropical forests: their richness in Coleoptera and other arthropod species. *Coleopt. Bull.* 36:74–75
 75. Feeny PP. 1976. Plant apparency and chemical defense. In *Biochemical Interactions Between Plants and Insects. Recent Advances in Phytochemistry*, ed. J Wallace, RL Mansell, 10:1–40. New York: Plenum
 76. Feibert EB, Langenheim JH. 1988. Leaf resin variation in *Copaifera langsdorfii*: relation to irradiance and herbivory. *Phytochemistry* 27:2527–32
 77. Fensham RJ. 1994. Phytophagous insect-woody sprout interactions in tropical eucalypt forest. II. Insect community structure. *Aust. J. Ecol.* 19:189–96
 78. Filip V, Dirzo R, Maass JM, Sarukhan J. 1995. Within- and among-year variation in the levels of herbivory on the foliage of trees from a Mexican tropical deciduous forest. *Biotropica* 27:78–86
 79. Fittkau EJ, Klinge H. 1973. On biomass and trophic structure of the Central Amazonian rainforest ecosystem. *Biotropica* 5:2–14
 80. Foley WJ, Hume ID. 1987. Passage of digesta markers in two species of arboreal folivorous marsupials: the greater glider (*Petauroides volans*) and the brushtail possum (*Trichosurus vulpecula*). *Physiol. Zool.* 60:103–13
 81. Forget PM. 1989. La regeneration naturelle d'une espece autochre de la foret guyanaise: *Eperua falcata* Aublet (Caesalpinaceae). *Biotropica* 21:115–25
 82. Forget PM. 1991. Comparative recruitment patterns of two non-pioneer canopy tree species in French Guiana. *Oecologia* 85:434–39
 83. Forget PM. 1992. Regeneration ecology of *Eperua grandiflora* (Caesalpinaceae), a large-seeded tree in French Guiana. *Biotropica* 24:146–56
 84. Forget PM. 1994. Recruitment pattern of *Vouacapoua americana* (Caesalpinaceae), a rodent-dispersed tree species in French Guiana. *Biotropica* 26:408–19
 85. Foster RB. 1982. Famine on Barro Colorado Island. See Ref. 132, pp. 201–12
 86. Foster RB. 1982. The seasonal rhythm of fruitfall on Barro Colorado Island. See Ref. 132, pp. 151–72
 87. Fowler HG. 1979. Seed predator responses. *Oecologia* 41:361–63
 88. Futuyma DJ. 1983. Evolutionary interactions among herbivorous insects and plants. In *Coevolution*, ed. DJ Futuyma, M Slatkin, pp. 207–31. Sunderland, MA: Sinauer
 89. Ganzhorn JU. 1992. Leaf chemistry and the biomass of folivorous primates in tropical forests. *Oecologia* 91:540–47
 90. Garcia-Guzman G, Dirzo R. 1991. Plant-pathogen-animal interactions in a tropical rain forest. *Am. Inst. Biol. Sci.* (Abstr.)
 91. Gaston KJ. 1993. Herbivory at the limits. *Trends Ecol. Evol.* 8:193–94
 92. Gershenzon J. 1994. The cost of plant chemical defense against herbivory. In *Insect-Plant Interactions*, ed. EA Bernays, 5:105–73. Boca Raton, FL: CRC
 93. Gilbert GS. 1995. Rainforest plant diseases: the canopy understory connection. *Selbyana* 16:75–77
 94. Gilbert GS, Hubbell SP, Foster RB. 1994. Density and distance-to-adult effects of a canker disease of trees in a moist tropical forest. *Oecologia* 98:100–8
 95. Gilbert LE, Singer MC. 1975. Butterfly ecology. *Annu. Rev. Ecol. Syst.* 6:365–97
 96. Givnish TJ. 1988. Adaptation to sun and shade: a whole-plant perspective. In *Ecology of Photosynthesis in Sun and Shade*, ed. JR Evans, S von Caemmerer, WW Adams III, pp. 63–92. CSIRO: Melbourne
 97. Gosz FR, Likens GE, Bormann FH. 1972. Nutrient content of litter fall on Hubbard Brook experimental forest, New Hampshire. *Ecology* 53:769–84
 98. Gould KS, Kuhn DN, Lee DW, Oberbauer SF. 1995. Why leaves are sometimes red. *Nature* 378:241–42
 99. Grime JP. 1979. *Plant Strategies and Vegetation Processes*. Chichester, UK: Wiley & Sons
 100. Harborne JB. 1979. Function of flavonoids in plants. In *Chemistry and Biochemistry of Plant Pigments*, ed. TW Goodwin, pp. 736–88. New York: Academic

101. Hladik A. 1978. Phenology of leaf production in rain forest of Gabon: distribution and composition of food for folivores. See Ref. 155, pp. 1–72
102. Hodkinson ID, Casson D. 1991. A lesser predilection for bugs: Hemiptera (Insecta) diversity in tropical rain forests. *Biol. J. Linn. Soc.* 43:101–9
103. Howe HF, Primack RB. 1975. Differential seed dispersal by birds of the tree *Casearia nitida* (Flacourtiaceae). *Biotropica* 7:278–83
104. Howe HF, Schupp EW. 1985. Early consequences of seed dispersal for a neotropical tree (*Virola surinamensis*.) *Ecology* 66:781–91
105. Howe HF, Smallwood J. 1982. Ecology of seed dispersal. *Annu. Rev. Ecol. Syst.* 13:201–28
106. Hubbell SP, Condit R, Foster RB. 1990. Presence and absence of density dependence in a neotropical tree community. *Philos. Trans. R. Soc. London Ser. B* 330:269–81
107. Hubbell SP, Foster RB. 1986. Commonness and rarity in a neotropical forest: implications for tropical tree conservation. In *Conservation Biology: The Science of Scarcity and Diversity*, ed. ME Soule, pp. 205–31. Sunderland, MA: Sinauer
108. Jaenike J. 1990. Host specialization in phytophagous insects. *Annu. Rev. Ecol. Syst.* 21:243–73
109. Janzen DH. 1970. Herbivores and the number of tree species in tropical forests. *Am. Nat.* 104:501–28
110. Janzen DH. 1971. Escape of juvenile *Dioclea megacarpa* (Leguminosae) vines from predators in a deciduous tropical forest. *Am. Nat.* 105:97–112
111. Janzen DH. 1972. Association of a rain-forest palm and seed-eating beetles in Puerto Rico. *Ecology* 53:258–61
112. Janzen DH. 1972. Escape in space by *Sterculia apetala* seeds from the bug *Dysdercus fasciatus* in a Costa Rican deciduous forest. *Ecology* 53:350–56
113. Janzen DH. 1973. Comments on host-specificity of tropical herbivores and its relevance to species richness. In *Taxonomy and Ecology*, ed. VH Heywood, pp. 201–11. New York: Academic
114. Janzen DH. 1974. Tropical blackwater rivers, animals and mast fruiting by the Dipterothripidae. *Biotropica* 6:69–103
115. Janzen DH. 1975. Interactions of seeds and their insect predators/parasitoids in a tropical deciduous forest. In *Evolutionary Strategies of Parasitic Insects and Mites*, ed. PW Price, pp. 154–86. New York: Plenum
116. Janzen DH. 1985. Plant defences against animals in the Amazonian rainforest. In *Amazonia*, ed. GT Prance, TE Lovejoy, pp. 207–17. Oxford/New York: Persimmon
117. Janzen DH, Miller GA, Hackforth-Jones J, Pond CM, Hooper K, Janos DP. 1976. Two Costa Rican bat-generated seed shadows of *Andira inermis* (Leguminosae). *Ecology* 57:1068–75
118. Kaczmarek W. 1967. Elements of organization in the energy flow of forest ecosystems (preliminary notes). In *Secondary Productivity in Terrestrial Ecosystems*, ed. K Petruszewica, pp. 683–85. Warsaw: Państwowe Wydawnictwo Naukowe
119. Karanth KU, Sunquist ME. 1992. Population structure, density and biomass of large herbivores in the tropical forests of Nagarohole, India. *J. Trop. Ecol.* 8:21–35
120. Kiltie RA. 1981. Distribution of palm fruits on a rain forest floor: Why white-lipped peccaries forage near objects. *Biotropica* 13:141–45
121. Kitajima K, Augspurger CK. 1989. Seed and seedling ecology of a monocarpic tropical tree, *Tachigalia versicolor*. *Ecology* 70:1102–14
122. Kleiber M. 1975. *The Fire of Life*. New York: Wiley & Sons. 453 pp.
123. Kursar TA, Coley PD. 1992. The consequences of delayed greening during leaf development for light absorption and light use efficiency. *Plant Cell Environ.* 15:901–9
124. Kursar TA, Coley PD. 1992. Delayed development of the photosynthetic apparatus in tropical rain forest species. *Funct. Ecol.* 6:411–22
125. Kursar TA, Coley PD. 1992. Delayed greening in tropical leaves: an anti-herbivore defense? *Biotropica* 24:256–62
126. Langenheim JH, Arrhenius SP, Nascimento JC. 1981. Relationship of light intensity to leaf resin composition and yield in the tropical leguminous genera *Hymenaea* and *Copaifera*. *Biochem. Syst. Ecol.* 9:27–37
127. Langenheim JH, Macedo CA, Ross MK, Stubblebine WH. 1986. Leaf development in the tropical leguminous tree *Copaifera* in relation to microlepidopteran herbivory. *Biochem. Syst. Ecol.* 14:51–59
128. Lawton JH. 1978. Host-plant influences on insect diversity: the effects of space and time. In *Diversity of Insect Faunas*, ed. LA Mound, N. Waloff, pp. 105–25.

- Oxford/London: Blackwell Sci.
129. Lee DW, Brammeier S, Smith AP. 1987. The selective advantages of anthocyanins in developing leaves of mango and cacao. *Biotropica* 19:40–49
 130. Lee MAB. 1985. Dispersal of *Panadanus tectorius* by the land crab *Cardisoma carnifex*. *Oikos* 45:169–73
 131. Leigh EG Jr. 1997. *Ecology of Tropical Forests: The View from Barro Colorado*. New York: Oxford Univ. Press
 132. Leigh EG Jr, Rand AS, Windsor DM, eds. 1982. *Ecology of a Tropical Forest: Seasonal Rhythms and Long-term Changes*. Washington, DC: Smithsonian Inst. Press. 468 pp.
 133. Leigh EG Jr, Wright SJ, Herre EA. 1993. The decline of tree diversity on newly isolated tropical islands: a test of a null hypothesis and some implications. *Evol. Ecol.* 7:76–102
 134. Levin DA. 1976. Alkaloid-bearing plants: an ecogeographic perspective. *Am. Nat.* 110:261–84
 135. Levin DA, York BM. 1978. The toxicity of plant alkaloids: an ecogeographic perspective. *Biochem. Syst. Ecol.* 6:61–76
 136. Lieberman D, Lieberman M. 1984. Causes and consequences of synchronous flushing in a dry tropical forest. *Biotropica* 16:193–201
 137. Lowman MD. 1984. An assessment of techniques for measuring herbivory: Is rainforest defoliation more intense than we thought? *Biotropica* 16:264–68
 138. Lowman MD. 1985. Temporal and spatial variability in insect grazing of the canopies of five Australian rainforest tree species. *Aust. J. Ecol.* 10:7–24
 139. Lowman MD. 1992. Herbivory in Australian rain forests, with particular reference to the canopies of *Doryphora sassafras* (Monimiaceae). *Biotropica* 24:263–72
 140. Lowman MD. 1993. Forest canopy research: Old World, New World comparisons. *Selbyana* 14:1–2
 141. Lowman MD, Box JD. 1983. Variation in leaf toughness and phenolic content among five species of Australian rain forest trees. *Aust. J. Ecol.* 8:17–25
 142. MacArthur R. 1967. Limiting similarity, convergence and divergence of coexisting species. *Am. Nat.* 101:377–85
 143. MacArthur RH. 1969. Patterns of communities in the tropics. *Biol. J. Linn. Soc.* 1:19–30
 144. Marquis RJ. 1984. Leaf herbivores decrease fitness of a tropical plant. *Science* 226:537–39
 145. Marquis RJ. 1991. Herbivore fauna of Piper (Piperaceae) in a Costa Rican wet forest: diversity, specificity, and impact. See Ref. 173, pp. 179–99
 146. Marquis RJ. 1992. A bite is a bite is a bite? Constraints on response to folivory in Piperarieianum (Piperaceae). *Ecology* 73:143–52
 147. Marquis RJ, Braker HE. 1994. Plant-herbivore interactions: diversity, specificity, and impact. In *La Selva: Ecology and Natural History of a Neotropical Rainforest*, ed. LA McDade, KS Bawa, HA Hespenheide, GS Hartshorn, pp. 261–81. Chicago/London: Univ. Chicago Press
 148. McKey DD. 1974. Adaptive patterns in alkaloids physiology. *Am. Nat.* 108:305–20
 149. McKey DD. 1979. The distribution of secondary compounds within plants. In *Herbivores: Their Interactions with Secondary Plant Metabolites*, ed. GA Rosenthal, DH Janzen, pp. 55–133. New York: Academic
 150. McKey DD. 1984. Interaction of the ant-plant *Leonardoxa africana* (Caesalpiniaceae) with its obligate inhabitants in a rainforest in Cameroon. *Biotropica* 16:81–99
 151. McKey DD, Waterman PG, Mbi CN, Gartlan SJ, Struhsaker TT. 1978. Phenolic content of vegetation in two African rain forests: ecological implications. *Science* 202:61–64
 152. McNab BK. 1978. Energetics of arboreal folivores: physiological problems and ecological consequences of feeding on an ubiquitous food supply. See Ref. 155, pp. 153–62
 153. Milton K. 1990. Annual mortality patterns of a mammal community in central Panama. *J. Trop. Ecol.* 6:493–99
 154. Mole S, Ross JAM, Waterman PG. 1988. Light-induced variation in phenolic levels in foliage of rain-forest plants. I. Chemical changes. *J. Chem. Ecol.* 14:1–21
 155. Montgomery GG, ed. 1978. *Ecology of Arboreal Folivores*. Washington, DC: Smithsonian Inst. 574 pp.
 156. Mooney HA, Chu C. 1974 Seasonal carbon allocation in *Heteromeles arbutifolia*, a California shrub. *Oecologia* 14:295–306
 157. Moran N, Hamilton WD. 1980. Low nutritive quality as a defense against herbivores. *J. Theor. Biol.* 86:247–54
 158. Murali KS, Sukumar R. 1993. Leaf flushing phenology and herbivory in a tropical dry deciduous forest, southern India. *Oe-*

- ecologia* 94:114–19
159. Nagy KA, Montgomery GG. 1980. Field metabolic rate, water flux, and food consumption in three-toed sloths (*Bradypus variegatus*). *J. Mamm.* 61:465–72
 160. Nascimento MT, Hay JD. 1993. Intraspecific variation in herbivory on *Metrodorea pubescens* (Rutaceae) in two forest types in central Brazil. *Rev. Brasil. Biol.* 53:143–53
 161. Newberry DM, de Foresta H. 1985. Herbivory and defense in pioneer gap and understorey trees in tropical rain forests in French Guiana. *Biotropica* 17:238–44
 162. Nichols-Orians CM. 1991. The effects of light on foliar chemistry, growth and susceptibility of seedlings of a canopy tree to an attine ant. *Oecologia* 86:552–60
 163. Nuñez-Farfan J, Dirzo R. 1989. Leaf survival in relation to herbivory in two tropical pioneer species. *Oikos* 55:71–74
 164. Oates JF, Whitesides GH, Davies AG, Waterman PG, Green SM, et al. 1990. Determinants of variation in tropical forest primate biomass: new evidence from West Africa. *Ecology* 71:328–43
 165. O'Dowd DJ. 1979. Foliar nectar production and ant protection on a neotropical tree, *Ochroma pyramidale*. *Oecologia* 43:233–48
 166. O'Dowd DJ, Willson MF. 1989. Leaf domatia and mites on Australasian plants: ecological and evolutionary implications. *Biol. J. Linn. Soc.* 37:191–236
 167. Opler PA, Frankie GW, Baker HG. 1980. Comparative phenological studies of treelet and shrub species in tropical wet and dry forest in the lowlands of Costa Rica. *J. Ecol.* 68:167–88
 168. Orians GH, Janzen DH. 1974. Why are embryos so tasty? *Am. Nat.* 108:581–92
 169. Osunkoya OO, Ash JE, Graham AW, Hopkins MS. 1993. Growth of tree seedlings in tropical rain forests of North Queensland. *J. Trop. Ecol.* 9:1–18
 170. Price PW. 1980. *Evolutionary Biology of Parasites*. Princeton, NJ: Princeton Univ. Press. pp. 105–33. 237 pp.
 171. Price PW. 1991. Patterns in communities along latitudinal gradients. See Ref. 173, pp. 51–69
 172. Price PW, Bouton CE, Gross P, McPherson BA, Thompson JN, Weis AE. 1980. Interactions among three trophic levels: influence of plants on interactions between insect herbivores and natural enemies. *Annu. Rev. Ecol. Syst.* 11:41–65
 173. Price PW, Lewinsohn TM, Fernandes GW, Benson WW, eds. 1991. *Plant-Animal Interactions: Evolutionary Ecology in Tropical and Temperate Regions*. New York: Wiley & Sons. 639 pp.
 174. Rehr SS, Feeny PP, Janzen DH. 1973. Chemical defense in Central American non-ant acacias. *Biochem. Syst.* 1:63–67
 175. Reich PB. 1995. Phenology of tropical forests: patterns, causes and consequences. *Can. J. Bot.* 73:164–65
 176. Reich PB, Uhl C, Walters MB, Ellsworth DS. 1991. Leaf lifespan as a determinant of leaf structure and function among 23 Amazonian tree species. *Oecologia* 86:16–24
 177. Rhoades DF, Cates RG. 1976. Toward a general theory of plant antiherbivore chemistry. In *Biochemical Interactions Between Plants and Insects. Recent Adv. Phytochem.*, ed. J Wallace, RL Mansell, 10:168–213. New York: Plenum
 178. Robbins CT. 1993. *Wildlife Feeding and Nutrition*. New York: Academic. 2nd ed.
 179. Sagers CL. 1992. Manipulation of host plant quality: herbivores keep leaves in the dark. *Funct. Ecol.* 6:741–43
 180. Sagers CL, Coley PD. 1995. Benefits and costs of defense in a neotropical shrub. *Ecology* 76:1835–43
 181. Schowalter TS, Crossley DA Jr. 1988. Canopy arthropods and their response to forest disturbance. In *Forest Hydrology and Ecology at Coweeta*, ed. TW Swank, DA Crossley Jr, pp. 207–18. New York: Springer-Verlag
 182. Schowalter TS, Webb JW, Crossley DA Jr. 1981. Community structure and nutrient content of canopy arthropods in clearcut and uncut forest ecosystems. *Ecology* 62:1010–19
 183. Schupp EW. 1988. Seed and early seedling predation in the forest understorey and in treefall gaps. *Oikos* 51:71–78
 184. Schupp EW, Feener DH Jr. 1991. Phylogeny, lifeform, and habitat dependence of ant-defended plants in a Panamanian forest. In *Ant-Plant Interactions*, ed. CR Huxley, DF Cutler, pp. 175–97. Oxford: Oxford Univ. Press
 185. Scriber JM. 1973. Latitudinal gradients in larval feeding specialization of the world Papilionidae (Lepidoptera). *Psyche* 80:355–73
 186. Smith AP, Mulkey SS, Chazdon RL, eds. 1996. *Tropical Forest Plant Ecophysiology*. New York: Chapman & Hall. 675 pp.
 187. Sork VL. 1987. Effect of predation and light on seedling establishment in *Gustavia superba*. *Ecology* 68:1341–50
 188. Southwood TRE, Brown VK, Reader

- PM. 1986. Leaf palatability, life expectancy and herbivore damage. *Oecologia* 70:544–48
189. Stamp NE, Casey TM, eds. 1993. *Caterpillars: Ecological and Evolutionary Constraints on Foraging*. New York: Chapman & Hall. 587 pp.
190. Sterck F, van der Meer P, Bongers F. 1992. Herbivory in two rain forest canopies in French Guyana. *Biotropica* 24:97–99
191. Stork NE. 1987. Guild structure of arthropods from Bornean rain forest trees. *Ecol. Entomol.* 12:69–80
192. Terborgh J, Emmons LH, Freese C. 1986. La fauna silvestre de la Amazonia: el despilfarro de un recurso de un renovable. *Bol. Lima* 46:77–85
193. Terborgh J, Losos E, Riley MP, Bolanos Riley M. 1993. Predation by vertebrates and invertebrates on the seeds of five canopy tree species of an Amazonian forest. *Vegetatio* 107/108:375–86
194. Terborgh J, van Schaik CP. 1987. Convergence vs. nonconvergence in primate communities. In *Organization of Communities*, ed. JHR Gee, PS Giller, pp. 205–26. Oxford: Blackwell Sci.
195. Terborgh J, Wright SJ. 1994. Effects of mammalian herbivores on plant recruitment in two neotropical forests. *Ecology* 75:1829–33
196. Traveset A. 1990. Post-dispersal predation of *Acacia farnesiana* seeds by *Stator vachelliae* (Bruchidae) in Central America. *Oecologia* 84:506–12
197. Turner IM. 1995. Foliar defences and habitat adversity of three woody plant communities in Singapore. *Funct. Ecol.* 9:279–84
198. Vandermeer JH. 1977. Notes on density-dependence in *Welfia georgii* Wendl. ex. Burret (Palmae) a lowland rainforest species in Costa Rica. *Brenesia* 10/11:9–15
199. van Schaik CP, Terborgh JW, Wright SJ. 1993. Phenology of tropical forest: adaptive significance and consequences for primary consumers. *Annu. Rev. Ecol. Syst.* 24:353–77
200. van Soest PJ. 1982. *Nutritional Ecology of the Ruminant*. Portland: Durham & Downey
201. Walter DE, O'Dowd DJ. 1992. Leaves with domatia have more mites. *Ecology* 73:1514–18
202. Walter DE, O'Dowd DJ. 1995. Beneath biodiversity: factors influencing the diversity and abundance of canopy mites. *Selbyana* 16:12–20
203. Waterman PG, Ross JAM, Bennett EL, Davis AG. 1988. A comparison of the floristics and leaf chemistry of the tree flora in two Malaysian rainforests and the influence of leaf chemistry on populations of colobine monkeys in the Old World. *Biol. J. Linn. Soc.* 34:1–32
204. Wilson DE, Janzen DH. 1972. Predation on *Scheelea* palm seeds by bruchid beetles: seed density and distance from the parent palm. *Ecology* 53:954–59
205. Wolda H. 1978. Fluctuations in abundance of tropical insects. *Am. Nat.* 112:1017–45
206. Wolda H. 1988. Insect seasonality: Why? *Annu. Rev. Ecol. Syst.* 19:1–18
207. Wood TK, Olmstead KL. 1984. Latitudinal effects on treehopper species richness (Homoptera: Membracidae). *Ecol. Entomol.* 9:109–15
208. Wright SJ. 1983. Dispersion of eggs by a bruchid beetle among *Scheelea* palm seeds and the effect of distance to the parent palm. *Ecology* 64:1016–21
209. Wright SJ. 1996. Phenological responses to seasonality in tropical forest plants. See Ref. 186, pp. 440–60
210. Wright SJ, van Schaik CP. 1994. Light and phenology of tropical trees. *Am. Nat.* 143:192–99



CONTENTS

EARLY HISTORY AND PROGRESS OF WOMEN ECOLOGISTS: Emphasis Upon Research Contributions, <i>Jean H. Langenheim</i>	1
FOREST CANOPIES: Methods, Hypotheses, and Future Directions, <i>Margaret D. Lowman, Philip K. Wittman</i>	55
EXTINCTION BY HYBRIDIZATION AND INTROGRESSION, <i>Judith M. Rhymer, Daniel Simberloff</i>	83
EVOLUTIONARY SIGNIFICANCE OF RESOURCE POLYMORPHISMS IN FISHES, AMPHIBIANS, AND BIRDS, <i>Thomas B. Smith, Skúli Skúlason</i>	111
MANAGEMENT OF THE SPOTTED OWL: A Case History in Conservation Biology, <i>Barry R. Noon, Kevin S. McKelvey</i>	135
HISTORICAL BIOGEOGRAPHY OF WEST INDIAN VERTEBRATES, <i>S. Blair Hedges</i>	163
TROUBLE ON OILED WATERS: Lessons from the <i>Exxon Valdez</i> Oil Spill, <i>R. T. Paine, Jennifer L. Ruesink, Adrian Sun, Elaine L. Soulanille, Marjorie J. Wonham, Christopher D. G. Harley, Daniel R. Brumbaugh, David L. Secord</i>	197
EVOLUTIONARY SIGNIFICANCE OF LOCAL GENETIC DIFFERENTIATION IN PLANTS, <i>Yan B. Linhart, Michael C. Grant</i>	237
RATES OF MOLECULAR EVOLUTION: Phylogenetic Issues and Applications, <i>David P. Mindell, Christine E. Thacker</i>	279
HERBIVORY AND PLANT DEFENSES IN TROPICAL FORESTS, <i>P. D. Coley, J. A. Barone</i>	305
MECHANISMS CREATING COMMUNITY STRUCTURE ACROSS A FRESHWATER HABITAT GRADIENT, <i>Gary A. Wellborn, David K. Skelly, Earl E. Werner</i>	337
NATURAL FREEZING SURVIVAL IN ANIMALS, <i>Kenneth B. Storey, Janet M. Storey</i>	365
DEMOGRAPHIC AND GENETIC MODELS IN CONSERVATION BIOLOGY: Applications and Perspectives for Tropical Rain Forest Tree Species, <i>E. R. Alvarez-Buylla, R. García-Barríos, C. Lara- Moreno, M. Martínez-Ramos</i>	387
GENE TREES, SPECIES TREES, AND SYSTEMATICS: A Cladistic Perspective, <i>A. V. Z. Brower, R. DeSalle, A. Vogler</i>	423
INCIDENCE AND CONSEQUENCES OF INHERITED ENVIRONMENTAL EFFECTS, <i>MaryCarol Rossiter</i>	451

RECRUITMENT AND THE LOCAL DYNAMICS OF OPEN MARINE POPULATIONS, <i>M. J. Caley, M. H. Carr, M. A. Hixon, T. P. Hughes, G. P. Jones, B. A. Menge</i>	477
WHEN DOES MORPHOLOGY MATTER? <i>M. A. R. Koehl</i>	501
ADAPTIVE EVOLUTION OF PHOTORECEPTORS AND VISUAL PIGMENTS IN VERTEBRATES, <i>Shozo Yokoyama, Ruth Yokoyama</i>	543
MICROBIAL DIVERSITY: Domains and Kingdoms, <i>David M. Williams, T. Martin Embley</i>	569
THE GEOGRAPHIC RANGE: Size, Shape, Boundaries, and Internal Structure, <i>James H. Brown, George C. Stevens, Dawn M. Kaufman</i>	597