BETWEEN-SPECIES DIFFERENCES IN LEAF DEFENSES OF TROPICAL TREES

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ABSTRACT: Rates of herbivory and patterns of leaf defense are presented for light-demanding and shade-tolerant tree species growing in a lowland rainforest in Panama. More than 85 percent of the annual leaf damage is due to grazing by insects. There are over three orders of magnitude difference between species in the rates of herbivory on mature leaves. More than 70 percent of this variation can be statistically explained by measured defenses. Species with little herbivore damage have tough, fibrous leaves with low concentrations of nitrogen and water. Tannin levels are not significantly correlated with herbivory. Shade-tolerant species have higher levels of defense and suffer less herbivory than species that require light gaps for establishment. This may be due to differences in inherent growth rates between species, with slow-growing species being better defended. Evidence is also presented showing a correlation between leaf lifetime and type of defense. Comparisons of general patterns of herbivory and plant defense are made between temperate and tropical forests.

INTRODUCTION

In this paper, I present patterns of herbivory and plant defenses observed in a lowland tropical forest, in an attempt to explain why some species are better defended than others. Initially, I will describe various plant characteristics that make leaves palatable to herbivores, and then present evolutionary arguments for why we might see differences in both type and amount of defense.

TROPIC/TEMPERATE COMPARISONS

Research was carried out in a lowland tropical rainforest on Barro Colorado Island (BCI) in Panama. The site is administrated by the Republic of Panama and the Smithsonian Institution, and has been protected from poachers and tree cutters since the 1920's. Most of the forest is at least 200 years old (Foster and Brokaw 1982).

Climate

Several aspects of the climate and forest are noteworthy since they contrast sharply with many temperate systems. First, seasonality is much less dramatic on BCI (Croat 1978; Leigh and others 1982). Temperatures average 25 ^{o}C year round, with much of the variation being diurnal. Annual rainfall is high (250 cm/yr), but includes a distinct 4-month dry season. The dry season is clearly important in the annual rhythms of both plants and animals; however, only a few tree species are completely deciduous, and insect abundances remain relatively high (Wolda 1978). In northern systems that experience much greater seasonal severity, environmental constraints on evergreenness and insect life cycles may play a much more dominant role in plant/herbivore interactions.

Light

In contrast to many shrub-dominated areas in the Western United States, light may be the most limiting and variable resource in the forest on BCI. The canopy is 30 to 40 m tall, reducing light levels at the forest floor to only 1 to 5 percent of full sunlight (Chazdon and Fetcher 1984). In comparison, light levels in gaps created by fallen trees can be dramatically higher. although light gaps comprise only about 5 percent of the area, the increased light levels make them important areas of productivity (Hubbell and Foster in press). Smaller breaks in the canopy create light flecks which can be the major source of carbon gain for plants below (Bjorkman and others 1972; Pearcy and Calkin 1983).

Accompanying the wide range of light conditions at the forest floor is a continuum in shade tolerance among different tree species (Whitmore 1978; Denslow 1980; Hartshorn 1980; Brokaw 1985). At one extreme are species found only in light gaps that rely on rapid germination and establishment once a gap is formed. At the other extreme are highly shade-tolerant species, that can persist for many years in the understory.

Diversity

Another important feature of the forest on BCI relative to temperate communities is its high species diversity. Per hectare, there is an average of 60 tree species with greater than 20 cm d.b.h. (Leigh 1982). This diversity has several interesting implications for herbivory. First, one might predict that there would be fewer specialist herbivores than in a less diverse community. Although there are no data with which to test this, my personal observations suggest the contrary: most leaf damage on BCI is done by relatively specialized insects. Another consequence of

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tropical forest diversity is that one cannot understand general defense patterns and effects on herbivory by studying the dominant few species in the community. There simply aren't a few dominant species. However, working in a diverse community helps avoid the problem that general patterns may simply be a consequence of phylogenetic constraints on the dominant species. If large numbers of unrelated species have converged on a particular set of effective defenses, this can be a strong argument for the effectiveness of those defenses.

Herbivores

In neotropical forests, the vast majority of leaf tissue is eaten by insect rather than vertebrate herbivores. On BCI, 85 percent of the leaf area eaten annually is consumed by insects (Leigh and Smythe 1978). Vertebrate herbivores, notably sloths, iguanas, howler monkeys, and tapirs are conspicuous, but consume relatively little leaf material. I would argue that in neotropical forests the major selective pressure for the evolution of plant defenses is, therefore, due to grazing by insects.

HERBIVORY AND DEFENSES

To document general community-wide patterns, I measured herbivory and defenses for 47 of the most common canopy tree species on BCI (Coley 1983). These species represented a range of shade tolerance, from species that were gap specialists to those that could tolerate deep shade. To facilitate measurements, I worked with saplings. All individuals were studied in gaps to control for environmental influences and the availability of herbivores.

Patterns of Herbivory

Patterns of herbivory were quantified as the rate of damage to mature leaves. Over 400 saplings and approximately 10,000 leaves were marked and rates of herbivory measured during 6-week periods in each of the early wet, late wet, and dry seasons (Coley 1983). I emphasize the importance of measuring herbivory as a rate: the percentage of leaf area removed per unit of time. Because leaf lifetimes for different species vary by orders of magnitude, leaves are available to herbivores for different amounts of time. Single measurements of the amount of standing crop damage would therefore be misleading.

Average rates of herbivory differed enormously between the 47 study species (fig. 1). The least susceptible species lost an average of 0.0003 percent of its leaf area per day compared to 0.85 percent for the most damaged species (Coley 1983). This is a difference among species of over three orders of magnitude, despite the fact that study individuals were growing as neighbors in the same microhabitat, and were susceptible to the same herbivores.

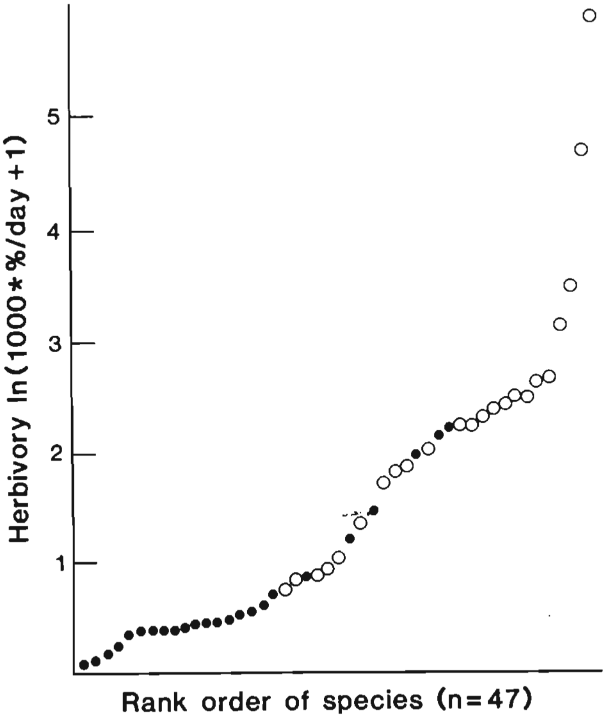

Figure 1.--Average annual rates of herbivory for mature leaves of 47 tree species on Barro Colorado Island, Panama. Herbivory measures are expressed as the natural log transformation of the percentage of leaf area consumed per day. Solid circles indicate shade-tolerant species, open circles indicate light-gap specialists.

Plant Defenses

Why are herbivores showing such strong preferences for certain species over others? To answer this, I measured leaf and plant properties that might influence rates of herbivory (Coley 1983) (table 1). Because it is impossible to measure all the secondary metabolites, I focused on a single widespread group: condensed tannins. There is considerable controversy surrounding the mode of action of tannins, but it is fairly well accepted that they serve some defensive function (Feeny 1970, 1976; Swain 1979; Bernays 1981; Martin and Martin 1982; Zucker 1983). I measured two forms of condensed tannins using the vanillin (VAN) and proanthocyanidin/BuOH (PRO) assays. Various components of fiber were also quantified (cellulose, acid-detergent fiber, neutral-detergent fiber, and lignin). Fiber provides structural support for the leaf, but it also reduces leaf digestibility for vertebrate and presumably invertebrate herbivores (Van Soest 1975; Milton 1979). Another measure related to fiber content is leaf toughness. This was measured as the amount of weight needed to punch a 3-mm rod through the leaf. Leaf pubescence was quantified as the density of hairs on the lower leaf surface. In addition to measuring potentially defensive properties, leaf nutritional value was estimated as the percentage of nitrogen and water.

Table 1.--Correlation coefficients for mature leaf characteristics and rates of herbivory for 47 canopy tree species on Barro Colorado Island, Panama. Values are the mean of several individuals for each species. Herbivory rates were measured throughout the year (Coley 1983)

Leaf characteristic	Correlation with herbivory
Tannin (VAN) % dw	-0.112
Tannin (PRO) % dw	-0.128
Fiber (NDF) % dw	-0.278 *
Fiber (ADF) % dw	-0.424 *
Lignin % dw	-0.223
Cellulose % dw	-0.473 *
Toughness (grams)	-0.515 *
Pubescence #/mm2	0.635 *
Water %	0.507 *
Nitrogen % dw	0.287 *

* Significant at P<0.05.

Table 1 correlates each leaf characteristic with herbivory. The magnitude of the correlation coefficient indicates the relative importance or effectiveness of each characteristic against herbivory. Water and nitrogen content were significantly positively correlated with herbivory. The various fiber components and the related toughness measure were all highly negatively correlated with herbivory. Tannin levels, however, showed no significant relationship to herbivory, and tannin/protein ratios were similarly uncorrelated. Pubescence was the only characteristic positively correlated with herbivory. This, along with its inverse relationship to other defenses, suggests that hairs may provide a simple way of identifying poorly defended species.

The results presented in table 1 show that species with tough, fibrous leaves of low nutritional value suffer the least amount of herbivory. Are these, however, the major leaf characteristics responsible for deterring herbivores? To examine this, I ran a multiple regression of herbivory as a function of the leaf characteristics mentioned above (Coley 1983). More than 70 percent of the variation in herbivory among species was statistically accounted for by differences in these leaf properties ($r=0.84$, $p<0.001$). This is an enormous amount of variation to explain for a natural system and suggests that nutritional and fiber contents are extremely important determinants of herbivory. Species not well defended by these measures are not escaping damage by other means (Rhoades and Cates 1976; Feeny 1976), but in fact are suffering high levels of herbivory.

BETWEEN-SPECIES DIFFERENCES IN DEFENSES

Defenses and Shade Tolerance

There is considerable variation among species in the extent of their defenses and in the resulting rates of herbivory. Are there any general defensive patterns, with certain groups of species tending to be better defended? For the species I studied on BCI, there were dramatic defensive differences related to the ability of each species to tolerate shade. In table 2, the 47 study species are divided into two categories based on their degree of shade tolerance. On average, species that were found only in light gaps were eaten six times more rapidly than shade-tolerant species. They had significantly lower concentrations of tannins, were less fibrous by all four measures, and only half as tough. In addition to being less well-defended, gap species had a higher nutritional value as measured by water and nitrogen contents.

Defenses and Growth Rate

The defensive differences between gap and shade-tolerant species (table 2) may be due to differences in inherent growth rates. Under the same microclimatic conditions, gap species grow more than twice as fast as shade-tolerant species (Coley 1983). Does the inherent growth rate of a species therefore show a relationship to the level of defense? For the 47 study species, there was a significant positive relationship between growth rate (annual height increase) and herbivory ($r=0.52$, $p<0.001$). This relationship was the same using other growth measurements such as annual leaf

Table 2.--Comparisons of mature leaf characteristics and rates of herbivory for 23 light-gap specialists and 24 shade-tolerant tree species on Barro Colorado Island, Panama. Values are the means for each species

Leaf characteristic	Light-gap specialist	Shade tolerant
Herbivory %/day	0.24	0.04 **
Tannin (VAN) % dw	0.8	2.4 *
Tannin (PRO) % dw	1.7	4.8 *
Fiber (NDF) % dw	41.3	51.1 *
Fiber (ADF) % dw	29.2	37.2 *
Lignin % dw	10.3	12.1
Cellulose % dw	17.4	23.4 *
Toughness (grams)	392	622 **
Water %	72	63 **
Nitrogen % dw	2.5	2.2 *

* significant at P<0.05
** significant at P<0.01

area production or maximum growth rate measured for an individual. There was also a significant negative relationship between growth rates and a linear combination of defenses (r=0.72, p<0.001). This indicated that the degree of investment in defenses was a function of inherent growth rate.

Conclusions

The general pattern that emerged from these data is that inherently slow-growing species show much higher investments in defense and consequently suffer much less herbivore damage. I and others argue that inherently slow growth rates select for high defense levels because the cost of defense is smaller and the impact of herbivory is potentially greater than for fast-growing species (Coley and others 1985; Gulmon and Mooney 1985). Inherent growth rates are determined evolutionarily by resource availability in the habitat to which a species is best adapted (Grime 1979; Chapin 1980). In my study, it was the shade-tolerant species that existed in resource-limited microhabitats and therefore had the slowest growth rates. Consequently they were also the best defended. This pattern of slow growers being better defended is also seen in areas where growth is limited by other resources such as water or nutrients (Brunig 1969; Janzen 1974; McKey and others 1978; Grime 1979; Bryant and Kuropat 1980; Bryant and others 1983; Coley and others 1985).

TYPE OF DEFENSE

The evidence presented above shows that slow-growing species tend to have greater amounts of defense, but makes no predictions concerning the type of defense. The diversity of plant secondary metabolites is enormous. Why are some species defended by tannins and others by alkaloids? What factors influence the type of chemical defense that will be used by different species? Part of the answer may be found by examining costs of different defenses under different conditions (McKey 1979, 1984; Coley and others 1985).

Traditionally, secondary compounds were considered inexpensive if they were present in low concentrations, and expensive if they occurred at high concentrations (Rhoades and Cates 1976; Feeny 1976). This ignores the potentially high cost associated with turnover (Coley and others 1985). Metabolically active compounds, such as alkaloids, cardiac glycosides, and mono- and di-terpenes can have half-lives on the order of hours or days (Robinson 1974; Waller and Nowacki 1978; Croteau and Johnson 1984). Although the pool size of these compounds is typically small, they have high rates of turnover. In other words, the plant must continually synthesize more compound to maintain the same concentration in the leaves. The cost of defense by these "mobile" compounds is therefore accumulated throughout the leaf life. This contrasts to "immobile" compounds such as fiber and tannins. There is an initial construction cost that can be high since they tend to be present in large concentrations. However, they are metabolically inactive, so there are essentially no continued costs associated with turnover (Walker 1975; Swain 1979). Because of their metabolic inactivity, immobile compounds cannot be withdrawn from the leaf at senescence (McKey 1979). For leaves with short leaf life, the cost of defending with mobile defenses is likely to be less than the cost of immobile ones (McKey 1984; Coley and others 1985). As leaf life time increases, the costs of defense by immobile compounds are expected to be less.

The above predictions are supported by data I obtained on BCI. Leaf life times were measured on 46 species, and ranged from an average of 4 months to over 3 years (Coley 1981). There is a significant positive correlation between the condensed tannin content and average leaf life of each species (r=0.46, p<0.005). There is also a significant positive correlation between total fiber content and leaf life (r=0.62, p<0.001). This suggests that species with longer lived leaves have higher investments in immobile defenses.

The distribution of immobile defenses observed for the BCI trees is what would be predicted based on cost/benefit analyses. What other constraints besides costs could influence the advantage of one type of defense over the other? Are there conditions under which we would expect to find mobile defenses in long-lived mature leaves, and how might these vary between the temperate and tropical zones? Unfortunately there are few data with which to test this, particularly from the tropics. Studies of temperate trees have shown that insect damage or environmental stress can induce short-term production of several classes of secondary compounds (Haukioja and Niemela 1979; Baldwin and Shultz 1983; Rhoades 1985). Most often these seem to be mobile compounds such as simple phenols and monoterpenes. Their production, even in species with long-lived leaves, would be effective against temporary outbreaks of herbivores. Once the outbreak passed, the resources contained in the mobile defenses could be reallocated to other functions. The cost would therefore only be incurred for a short period. Hypothetically then, if short-term induction is a response to herbivory, and if insect outbreaks are more common in the temperate zone compared to the aseasonal tropics, one might expect induction of defenses to also be more common in the temperate zone.

Another condition that might favor mobile defenses in mature long-lived leaves is a strong seasonality of herbivore populations. Variation in the types and numbers of herbivores could make different defenses advantageous at different times of the year. Many temperate evergreen trees suffer primarily from insect herbivores in the summer and vertebrate grazers in the winter. This type of seasonality in herbivores is not generally as pronounced in the humid neotropics.

A final condition likely to favor mobile defenses is seasonality in nutrient availability. If nutrients are primarily taken up at a time of year when growth demands are low, they must be temporarily stored. Mobile defenses would be a good form of storage (Mooney and others 1983).

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