

## FOOD QUALITY, COMPETITION, AND PARASITISM INFLUENCE FEEDING PREFERENCE IN A NEOTROPICAL LEPIDOPTERAN

THOMAS A. KURSAR,<sup>1,2,3</sup> BRETT T. WOLFE,<sup>2</sup> MARY JANE EPPS,<sup>2</sup> AND PHYLLIS D. COLEY<sup>1,2</sup>

<sup>1</sup>Department of Biology, University of Utah, Salt Lake City, Utah 84112 USA

<sup>2</sup>Smithsonian Tropical Research Institute, Balboa, Panama

**Abstract.** We surveyed Lepidoptera found on 11 species of *Inga* (Fabaceae:Mimosoideae) co-existing on Barro Colorado Island, Panama, to evaluate factors influencing diet choice. Of the 47 species of caterpillars (747 individuals) recorded, each fed on a distinct set of *Inga*. In the field, 96% of the individuals were found on young leaves. Growth rates of caterpillars that were fed leaves in the laboratory were 60% higher on young leaves compared to mature leaves. When caterpillars were fed leaves of nonhost *Inga*, they grew more slowly. These data provide support for a link between preference and performance. However, among hosts on which larvae normally occurred, faster growth rates were not associated with greater host electivity (the proportion of larvae found on each host species in the field, corrected for host abundance). Growth rates on normal hosts were positively correlated with leaf expansion rates of the host, and fast expansion was associated with leaves with higher nutritional content. Detailed studies on a gelechiid leaf roller, the species with the largest diet breadth, allowed us to assess the importance of factors other than growth that could influence diet electivity. This species showed a 1.7-fold difference in growth rate among *Inga* hosts and faster growth on species with fast-expanding leaves. However, there was no correlation between caterpillar growth rate and abundance on different host species. Instead, abundance of the gelechiid on each *Inga* species was significantly correlated with the temporal predictability of food (synchrony of leaf flushing) and was negatively correlated with competition (amount of leaf area removed by species other than the gelechiid). Although rates of parasitism were high (23–43%), there were no differences among hosts. Parasitism was also not related to measures of escape, such as growth rates of caterpillars, leaf expansion rates, and synchrony of leaf production. Together, food availability, parasitism, and competition explained 84% of the variation in host preference by the gelechiid. We suggest that these ecological interactions may be particularly important in determining diet choice initially and that preferences may be reinforced by subsequent divergence in host chemistry and/or the herbivore's ability to tolerate the secondary metabolites.

**Key words:** competition; electivity; gelechiid; herbivore growth; *Inga*; leaf expansion; leafing phenology; Lepidoptera; Panama; parasitism; plant quality.

### INTRODUCTION

Diet choice by herbivorous insects involves the integration of many factors that could affect their fitness. Plant secondary chemistry has long been thought to be central in restricting host use and driving a coevolutionary arms race between herbivores and plants (Ehrlich and Raven 1964, Bazzaz 1997). However, other factors such as competition among herbivores and herbivore escape from natural enemies may also influence diet choice (Price et al. 1980, Harrison and Karban 1986, Lill et al. 2002, Singer and Stireman 2003, Bezzerides et al. 2004, Viswanathan et al. 2005). In addition, host-plant traits such as nutritional quality, physical and chemical defenses, and the phenology of leaf production can directly affect herbivore growth and survival, as well as influence interactions with compet-

itors and enemies. Thus diet selection by insect herbivores reflects the interactions and trade-offs among many ecological factors.

Here we report on the relationship between caterpillar growth rates and host use for the community of Lepidoptera feeding on a single neotropical genus of tree, *Inga* (Fabaceae) in a tropical moist forest in Panama. Because caterpillar growth rates may not be the major factor determining host use, we also explore the effect of food quality, availability, competition, and parasitism on diet selection or electivity for one common caterpillar that fed on 10 species of *Inga*. We focused on leaf damage caused by Lepidoptera, as they are responsible for the majority of the herbivory suffered by rain forest plants (Janzen 1988, Barone 1998, Novotny et al. 2004), including *Inga*. By investigating herbivore use of related plants at a single site, we may gain insight into factors affecting diet choice that, in comparisons of species that have evolved distinct secondary metabolites, may be masked.

Manuscript received 16 December 2005; revised 1 June 2006; accepted 5 June 2006. Corresponding Editor: M. D. Eubanks.

<sup>3</sup> E-mail: kursar@biology.utah.edu

Food quality affects insect performance in the laboratory and has been shown to shape diet preference in the field (Mattson 1980, Rausher 1981, Scriber and Slansky 1981, Raupp and Denno 1983, Osier and Lindroth 2001, Holton et al. 2003). Food quality is partially determined by defenses, primarily toughness and secondary metabolites, but also by nutrients, primarily water and nitrogen. In the tropics, most herbivory occurs on young leaves, which are more nutritious than mature leaves (Coley and Barone 1996). Within young leaves from both the Old and New World tropics, rates of damage vary 5–10 fold among species at a single site. This variation is positively correlated with leaf expansion rates (Coley and Kursar 1996, Kursar and Coley 2003). Although rapid expansion shortens the window of vulnerability when leaves are tender (Aide and Londoño 1989), rapid expansion requires high concentrations of nitrogen associated with growth processes (Kursar and Coley 1991, 1992*a, b, c*). In addition, in order to expand quickly, resources are shifted from defense to growth (Kursar and Coley 2003, Brenes-Arguedas et al. 2006). Thus, the higher rates of occurrence of herbivores on fast expanders can be explained by their higher nitrogen content and less effective chemical defenses (Kursar and Coley 2003, Coley et al. 2005). We predicted that these trends would hold within a single genus, *Inga*, and that caterpillar growth rates would be correlated with food quality and hence expansion rate of host leaves.

Also, the risk of predation or parasitism on different hosts appears to determine host use (Price et al. 1980, Bernays 1989, Coley et al. 2005), and recent studies have shown differences in herbivore susceptibility to natural enemies when feeding on different hosts (Bjorkman et al. 1997, Ballabeni et al. 2001, Barbosa et al. 2001, Lill et al. 2002, Murphy 2004). Furthermore, the slow growth-high mortality hypothesis suggests that the slower larvae grow, the longer they are susceptible to enemies, resulting in increased rates of predation and parasitism (Benrey and Denno 1997).

Although competition among herbivores was originally thought to be unimportant (Strong et al. 1984), it is now evident that food can be limiting and that competition can have large effects on herbivore numbers (Denno et al. 1995). Denno et al. point out that, relative to other herbivores, leaf feeders may experience the least competition. However, we suggest that, in the tropics, competition among young-leaf feeders could be particularly intense, as young leaves lose an average of 30% (range of 12–70%) of their leaf area in only a few weeks (Coley and Barone 1996, Kursar and Coley 2003).

Lastly, the availability or predictability of food might influence diet preference. Although all the *Inga* species were common at the study site, they differed with respect to leaf expansion rate and synchrony of young-leaf production, two traits that could affect the ability of herbivores to track their food. Thus, we predicted that variation among hosts in larval growth rate, as well as in

the above-mentioned ecological interactions, would correlate with host use in the field.

## METHODS

### *Study site*

Our study was conducted on Barro Colorado Island (BCI), Panama (9° N, 80° W), a research station operated by the Smithsonian Tropical Research Institute. The forest is classified as a tropical, moist forest and there is a four-month dry season from mid-December until mid-April (Holdridge et al. 1971, Croat 1978, Leigh 1999).

### *Plant species*

We collected caterpillars among 11 species of *Inga* (Fabaceae), a neotropical genus of trees that is common on BCI. The genus *Inga* is speciose (Pennington 1997), and noncoding nuclear ribosomal and chloroplast DNA sequence data are consistent with recent diversification (Richardson et al. 2001, Lavin 2006). Seventeen species of BCI flora are listed. Species not included in our study are those that are rare or restricted to the laboratory clearing or lakeshore.

Almost all species of caterpillars were found predominantly on young leaves (see Plate 1). Leaf expansion times ranged from fast to slow, and some plants produced leaves continuously while others flushed synchronously. We analyzed several characteristics that have been shown to be relevant to leaf development and herbivore attack: synchrony of leaf production, expansion rates of young leaves, and nitrogen and water contents. Not all data were collected on all plant species. To measure the young-leaf expansion rate, we marked freshly emerged leaves (<10% expanded) and measured their area with plastic grids every 48 h until the leaves stopped expanding. We calculated the daily percentage increase in size during the expansion phase using the following equation: Expansion rate as percent per day =  $100 \times [\exp(\ln(\text{area2}/\text{area1})/\text{time}) - 1]$  where “area1” and “area2” are leaf areas at two different measurements and “time” equals the number of days between measurements. Values of 100% per day indicate that the leaves doubled in size daily.

The production of young leaves for nine *Inga* was monitored monthly for 50 individual plants of each species from March 2001 to November 2004 (scored as presence/absence). The coefficient of variation (cv) for the percentage of individuals leafing each month was used to quantify synchrony in leaf production. Higher values indicate greater synchrony.

To measure nitrogen content and water content, we collected young leaves that were 50% expanded and dried them at 55°C to obtain the dry mass. Freeze-dried leaves from at least five individuals were pooled and run in duplicate to determine nitrogen content using an isotope ratio mass spectrometer (Finnigan MAT Delta S, San Jose, California, USA).

TABLE 1. Host electivity of caterpillars found on 11 species of *Inga*.

<i>Inga</i> spp.	No. plants	Gele1	Phoar	Nymha	Noct1	Thec1	Thehe	Pyra1	Synmy	micr1	micr2	Lyca2	Damage
<i>I. acuminata</i>	162	0	0	1	0	0	0	5	7	0	0	0	23.3
<i>I. cocleensis</i>	186	<b>14</b>	0	0	0	0	0	0	6	0	0	0	23.6
<i>I. goldmanii</i>	156	<b>13</b>	9	1	0	20	17	<b>21</b>	7	<b>72</b>	0	0	22.8
<i>I. laurina</i>	98	6	7	9	<b>20</b>	<b>32</b>	0	0	0	0	0	39	31.4
<i>I. marginata</i>	254	6	0	<b>22</b>	4	0	0	7	4	0	<b>100</b>	<b>61</b>	40.6
<i>I. multijuga</i>	148	<b>11</b>	0	1	0	0	0	<b>28</b>	<b>52</b>	0	0	0	42.5
<i>I. nobilis</i>	140	8	<b>21</b>	<b>40</b>	14	22	39	0	8	0	0	0	24.3
<i>I. pezizifera</i>	284	9	<b>18</b>	<b>20</b>	14	0	0	<b>24</b>	12	0	0	0	25.4
<i>I. sapindoides</i>	120	<b>15</b>	6	0	0	0	0	7	0	0	0	0	22.4
<i>I. umbellifera</i>	246	2	9	7	<b>48</b>	26	<b>44</b>	0	5	0	0	0	20.5
<i>I. vera</i>	199	<b>17</b>	<b>30</b>	0	0	0	0	8	14	28	0	0	34.4
No. records	1983	430	22	114	21	10	7	22	16	5	18	10	

Notes: Electivities (host preferences) were calculated separately for each species of caterpillar. Specifically, the number of caterpillar records on each species of *Inga* was divided by the number of plants with young-leaf flushes that were inspected for herbivores, giving the number of records per flush. These were summed across all 11 *Inga* species and converted to percentages. For example, for *Thecla hemon* the number of records on *I. goldmanii*, *I. nobilis*, and *I. umbellifera* (1, 2, and 4, respectively) was divided by the number of flushes inspected (156, 140, and 246, respectively). These three values were converted to percentages, giving 17%, 39%, and 44% of the *Thecla hemon* records on the three, respective, *Inga* species. Values in boldface, with high electivity, were considered preferred hosts. All caterpillars with  $\geq 10$  records (nine species) plus two species used in feeding trials are included. Columns are as follows: *Inga* species, the number of plants with young-leaf flushes that were inspected for herbivores (number of plants), followed by the codes and electivities for 11 caterpillar species, and the percentage of leaf area removed by all herbivores and pathogens during leaf expansion (damage). The bottom row (number of records) indicates numbers of leaf flushes sampled and herbivore records. Caterpillar morphospecies were clustered based on the similarity of their host use (SAS, CLUSTER procedure). For the caterpillar morphospecies, the abbreviations, taxonomy, and the morphospecies codes (in parentheses) as listed in our database are as follows: Gele1, Gelechiidae (LRBH); Phoar, *Phoebis argante*, Pieridae (HL76); Nympha, *Nymphidium haematostichum*, Riodinidae (HL53); Noct1, Noctuidae (HL19); Thec1, Lycaenidae (HL146); Thehe, *Thecla hemon*, Lycaenidae (HL27); Pyra1, leaf-rolling Pyralidae (HL77); Synmy, *Synargis mycone*, Riodinidae (HL33); micr1 (HL25) and micr2 (HL160) are microlepidopteran leaf rollers; Lyca2, Lycaenidae (HL93). *Inga* nomenclature follows Pennington (1997). In Croat (1978), *I. laurina* is listed as *I. jagifolia*, and *I. nobilis* is listed as *I. quaternata*.

#### Lepidopteran collection and rearing

To determine host use, we recorded presence/absence of morphospecies on 1893 flushes of young *Inga* leaves produced from August 2004 to July 2005 on saplings between 0.5 and 3 m in height located in the shaded understory. We did not record the number of individuals of each morphospecies on each flush. We had 747 records of 39 species of caterpillar on 11 *Inga* species (*Inga* species are listed in Table 1 and caterpillar morphospecies are listed in Appendix A). Our collection periods included both the dry and wet seasons. For each caterpillar, we recorded the plant species and leaf age for the leaf on which it was feeding. We photographed and reared specimens, and we entered them into our database. Using larvae and adult specimens, we identified the lepidopterans to the lowest taxon possible (most to family and some to species). Voucher specimens are stored on BCI, and some duplicate specimens are with experts for identification.

Using a growth chamber (25°C, 12 h light; Percival I-35LL, Boone, Iowa, USA) to control light and

temperature, we reared 489 caterpillars of 42 different species. Each individual was placed in a separate Petri dish (60 mm  $\times$  15 mm) and fed leaves of the same species and age as those on which they were initially found. In addition, for common species, we switched caterpillars to nonhost leaves and measured growth. Leaves were replaced with fresh ones at least every other day. To calculate relative growth rates, we weighed caterpillars every 24–48 h. For each healthy individual, we averaged its change in mass between measurements and divided the average by the midpoint mass to get an individual relative growth rate (grams per gram per day). The negative mass gains just before pupation were dropped. We averaged relative growth rates for all the individuals of the same caterpillar species feeding on the same leaf age of the same species of plant to get a mean relative growth rate for each caterpillar–host combination. Larval growth rate is widely used as an indicator of performance. It is generally positively correlated with pupal mass and negatively correlated with development time (Osier and Lindroth 2004).

TABLE 2. Relative growth rates ( $\text{g}\cdot\text{g}^{-1}\cdot\text{d}^{-1}$ ) for larvae feeding on *Inga*, the host on which they are typically found (high electivity, indicated by boldface in Table 1) vs. hosts on which they were infrequently found (low electivity) (paired *t* test,  $t = 0.29$ ,  $df = 7$ , NS).

Species	High electivity ( <i>N</i> )	Low electivity ( <i>N</i> )	Nonhost ( <i>N</i> )	No. caterpillars
Gele1	0.364 (5)	0.324 (5)	0.037 (1)	124
Nymha	0.322 (3)	0.250 (3)	0.142 (2)	57
Pyra1	0.345 (3)	0.249 (4)	0.247 (2)	54
Phoar	0.585 (3)	0.470 (4)		28
Noct1	0.441 (2)	0.397 (2)		14
Thehe	0.533 (1)	0.528 (1)		10
Synmy	0.176 (1)	0.327 (6)		12
micr1	0.381 (1)	0.528 (1)		11

Notes: For three species we switched caterpillars to nonhost *Inga* and compared growth with normal hosts (paired *t* test,  $t = 2.98$ ,  $df = 4$ ,  $P < 0.05$ , 5 host-caterpillar combinations, 26 individuals). "*N*" is number of host species. (See Table 1 for names of caterpillar species and levels of host electivity.)

Caterpillars were collected opportunistically and represented a range of instars. However, there was no effect of initial larval mass on subsequent growth rates ( $r^2 = 0.00$ ,  $P = 0.3$ ,  $n = 145$ ). There was also no effect of initial mass on larval growth in feeding trials with a leaf-rolling gelechiid when larvae were switched to novel hosts ( $r^2 = 0.06$ ,  $P = 0.9$ ,  $n = 19$ ). And, our collections of primarily early instars did not eliminate parasitism. In fact, caterpillars from which parasitoids ultimately emerged had lower initial masses than those that were not parasitized (0.0032 g vs. 0.0054 g,  $t = 2.17$ ,  $P = 0.03$ ,  $n = 221$ ).

To quantify host preference (Hassell and Southwood 1978, Crawley 1983), we used an electivity index (Singer 2000). In order to correct for plant abundance, host preference was calculated for each caterpillar morpho-species as the number of records for each species of *Inga* divided by the number of *Inga* plants of that species with flushes that were inspected, giving the number of records per flush. The percentage of individuals of an herbivore species on each host gives a measure of its electivity (summing to 100% across all hosts). See Table 1 for a sample calculation. Electivity is a combination of host availability, behavioral oviposition preferences, and subsequent ecological interactions for the caterpillars. Electivity is equivalent to the term "preference" or the term "host use" (Hassel and Southwood 1978, Crawley 1983).

To assess the effects of growth, food availability, competition, and parasitism on host use, we focused on a common leaf-rolling Gelechiidae that feeds on young leaves of a variety of *Inga* species. Because of the difficulty of identification in this family, we do not have a definite species name. However, DNA sequence data were used to evaluate the relevance of our morphotype identifications for species-level distinctions. Congeneric species typically exceed 3% divergence in the rapidly evolving mitochondrial gene cytochrome oxidase I (COI) (Hebert et al. 2003), but sequences from 35 of 36 individuals sampled from the 10 *Inga* hosts plus *Cojoba rufescens* (Fabaceae) grouped together with 98% similarity (L. Higgins and T. A. Kursar, unpublished

data), indicating the gelechiid morphotype consists of one species rather than a cryptic species complex. Similar analyses for two other common species confirmed our morphological classifications (Table 1: *Nymphidium haematostichum*, Riodinidae; and a leaf-rolling Pyralidae, Pyra1).

Host use by the gelechiid was estimated by recording the presence or absence of caterpillars on 1893 flushes produced from August 2004 to July 2005. The leaf roller was also occasionally found on other Fabaceae, but these data were not used to calculate relative abundance among *Inga* hosts. The synchrony of leafing (cv, see *Methods: Plant species*) was used as an index of the reliability or availability of suitable food. We collected caterpillars within a range of instars and reared 157 individuals in the laboratory to quantify rates of parasitism. Most parasitism was by a single wasp species with other wasp and fly parasitoids being much less common. To evaluate the extent of competition with other herbivores, we measured the amount of young-leaf area removed from different hosts by pathogens and herbivores other than the gelechiid (percent leaf area damaged during leaf expansion on 252 plants and 1063 leaves, June–November 2004). Gelechiids make distinct patterns of damage that can be distinguished from patterns of damage produced by all other sources. Total damage from all sources (percent leaf area lost during expansion) is listed in Table 1. Total damage was measured monthly on new leaves produced between February 2000 and November 2004 (over 100 individuals per species, 6216 leaves total).

#### Statistical analyses

We analyzed our data with SAS (SAS Institute 1999–2000). To examine similarity in host use, we clustered herbivores using PROC CLUSTER. Caterpillar growth rates fit assumptions of normality and were not transformed. Growth rates of herbivores on different hosts (Table 2) were compared using a paired *t* test corrected for unequal variances (hosts with high vs. low electivity and normal hosts vs. nonhosts). To determine if rates of parasitism for the gelechiid differed on

different plant species, we used a categorical ANOVA (CATMOD). Traits of the gelechiid (e.g., growth) and of the *Inga* species (e.g., flushing synchrony) were compared using simple and multiple regression models.

## RESULTS

### *Caterpillar host use and performance*

A total of 39 morphospecies were identified on 11 species of *Inga* during 12 monthly censuses (see *Methods*). Total lepidopteran species richness on the 11 BCI *Inga* species was estimated without randomizing sample order as  $51.2 \pm 7.3$  species (mean  $\pm$  SD; Chao 2; Colwell 2005); and  $53.7 \pm 8.6$  species; Jackknife 1; Colwell 2005). Many caterpillars were only found on one species of *Inga*, however this was driven by the large number of singleton collections (13 out of 39 species; Appendix B). Use of multiple hosts was common. After removing singletons from the analysis, four species used a single host and 22 species used more than one. For the nine most common caterpillar species (collected from  $\geq 10$  individual plants), host use was distinctly different among species (Table 1). Although most caterpillar species fed on a number of *Inga*, they also demonstrated considerable discrimination among hosts.

In feeding trials, we found substantial differences in growth rates of different caterpillar species feeding on the same *Inga* species (Fig. 1). For example, on *I. pezizifera*, *Phoebis argante* (Phoar) grew twice as fast as *Synargis mycone* (Synmy). In addition, the same caterpillar species differed in growth across different host species. (See Table 1 for species abbreviations.) *Nymphidium haematostichum* (Nympha) was found on six hosts and had growth rates ranging from 0.18 to 0.46  $\text{g}\cdot\text{g}^{-1}\cdot\text{d}^{-1}$ . In contrast, Pyra1 had rather similar growth rates across all six hosts (0.32–0.40  $\text{g}\cdot\text{g}^{-1}\cdot\text{d}^{-1}$ ).

To test if caterpillars grew best on their typical hosts, we compared growth on different hosts for the most common caterpillars (Table 2). There was no difference in growth rates on hosts on which caterpillars were commonly vs. uncommonly found (paired  $t = 0.22$ ,  $n = 8$  species of herbivores, NS) and there was no mortality. However, in all cases when we transferred caterpillars to an *Inga* host on which they were never recorded, they grew more slowly (Table 2; paired  $t$  test,  $t = 2.98$ ,  $\text{df} = 4$ ,  $P < 0.05$ ; 5 host–caterpillar combinations, 26 individuals). They also grew more slowly, in five of the seven cases, when they were transferred from the species on which they were collected to another species on which they were known to feed (data not shown; paired  $t = 2.17$ ,  $\text{df} = 6$ ,  $P = 0.07$ , 7 host–caterpillar combinations, 83 individuals). When we switched caterpillars, mortality increased, although it was not different between hosts with high or low electivity or nonhosts (25%, 33% and 22%, respectively).

Of the 489 individual caterpillars collected, only 20 were found on mature leaves, representing 6 of the 44 species. The overwhelming occurrence on young leaves is reflected in performance. Relative growth rate was

40% faster when caterpillars were feeding on young vs. mature leaves (young:  $0.39 \pm 0.014 \text{ g}\cdot\text{g}^{-1}\cdot\text{d}^{-1}$  [mean  $\pm$  SE],  $n = 98$ ; mature:  $0.24 \pm 0.027 \text{ g}\cdot\text{g}^{-1}\cdot\text{d}^{-1}$ ,  $n = 9$ ;  $t$  test,  $t = 3.19$ ,  $P < 0.005$ ). Even for the four species of caterpillar that were naturally found on both young and mature leaves, growth was 25% faster on young leaves (paired  $t = 7.3$ ,  $P < 0.01$ ).

### *Caterpillar growth rates on young leaves with different expansion rates*

Among young leaves, larval growth also differed across hosts. Leaf expansion rate was positively correlated with the relative growth rates of caterpillars (Fig. 2,  $r^2 = 0.35$ ,  $P = 0.032$ ,  $n = 11$  host species). That may be in part because fast-expanding young leaves are more nutritious. Expansion rate was positively correlated with water content ( $r^2 = 0.43$ ,  $P = 0.02$ ,  $n = 11$ ) and marginally so with nitrogen ( $r^2 = 0.19$ ,  $P = 0.10$ ,  $n = 11$ ). Growth rates were also positively correlated with water content ( $r^2 = 0.06$ ,  $P = 0.01$ ,  $n = 98$ ) but not with nitrogen content.

### *Does larval performance determine host electivity?*

To further explore the relationship between performance and host use, we examined host choice in an unnamed, leaf-rolling caterpillar in the family Gelechiidae. DNA sequence data showed those caterpillars to be of a single species (see *Methods*). That was the most common caterpillar, present on 23% of the *Inga* flushes and accounting for 58% of all lepidopteran records on *Inga*, which had the broadest diet of all the *Inga* feeders (10 hosts). Growth on normal hosts varied by a factor of 1.7 and was positively correlated with leaf water content ( $r^2 = 0.60$ ,  $P < 0.01$ ,  $n = 10$ ) and was slightly higher on plants with higher nitrogen contents ( $r^2 = 0.20$ ,  $P < 0.11$ ,  $n = 10$ ) and faster expansion rates ( $r^2 = 0.23$ ,  $P < 0.09$ ,  $n = 10$ ). The gelechiid's abundance in the field on its 10 hosts varied considerably (from 5 to 45% occupancy). However, there was a trend for larval abundance to be negatively correlated with larval growth in the laboratory feeding trials (Fig. 3A;  $r^2 = 0.28$ ,  $P < 0.069$ ,  $n = 10$ ). The four host plants on which larval abundance was the least in the field were the fast-expanding *Inga* species on which the gelechiid had grown well in the laboratory.

### *Do ecological interactions determine host electivity?*

To evaluate other factors that might influence the gelechiid's abundance on different hosts, we quantified the temporal availability of young leaves. We predicted that species that produced leaves more frequently would be a more reliable, and hence preferred, food source, as compared to species that produced leaves in a few synchronous flushes during the year. For each *Inga* species, we estimated the synchrony of leaf production as the cv in the percentage of plants flushing each month across three years. That ranged from 67% for *I. cocleensis*, a species in which leaf production occurred during most months of the year, to 143% for *I. laurina*, a

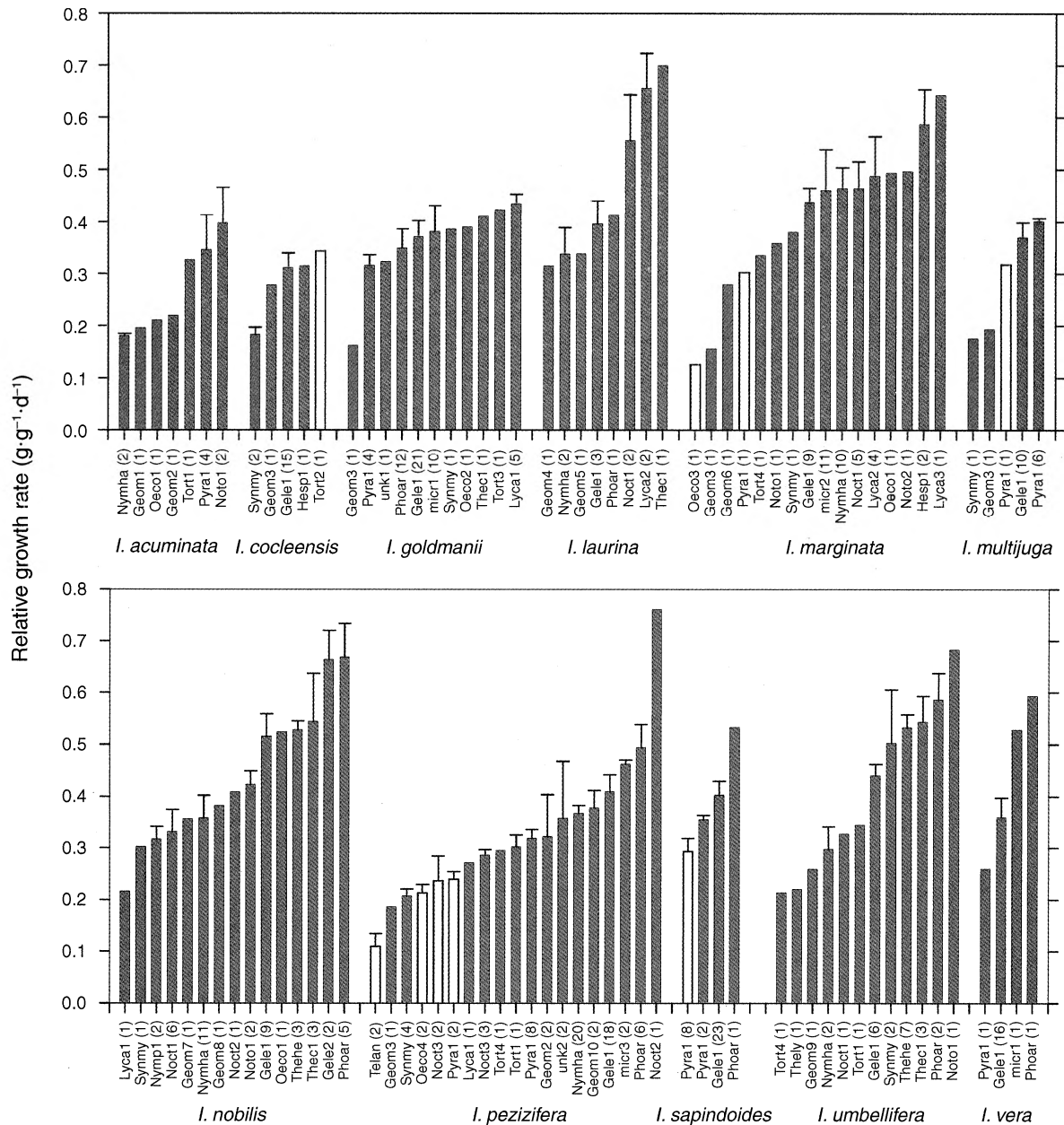


FIG. 1. Relative growth rates (g·g<sup>-1</sup>·d<sup>-1</sup>) of caterpillars reared on 11 *Inga* species. Caterpillars were reared on leaves of the same age and from the same host on which they were collected. Gray bars represent caterpillars reared on young leaves; white bars represent caterpillars reared on mature leaves. The abbreviations for the caterpillar species correspond to morphospecies, which are photographed and registered in our database. Database codes corresponding to the abbreviations are given in Appendix A.

species that produced leaves in 2–3 highly synchronous pulses each year. There was a significant negative relationship between the gelechiid’s abundance and the cv for leaf flushing, with *Inga* species that flush frequently being preferred (Fig. 3B;  $r^2 = 0.81$ ,  $P < 0.002$ ,  $n = 8$ ).

To see if the rate of parasitism correlated with the gelechiid’s host use, we raised 157 of the gelechiid caterpillars from the 10 different *Inga* hosts. There was

no significant difference in parasitism among hosts (ANOVA, NS) and no relationship between parasitism and abundance (Fig. 3C;  $r^2 = 0.00$ ,  $P = 0.99$ ,  $n = 10$ ). Parasitism was also not significantly correlated with flushing synchrony (cv) or expansion rate of young leaves.

To assess the impact of interspecific competition on host use, we calculated the amount of leaf area removed by pathogens and herbivores other than the gelechiid for

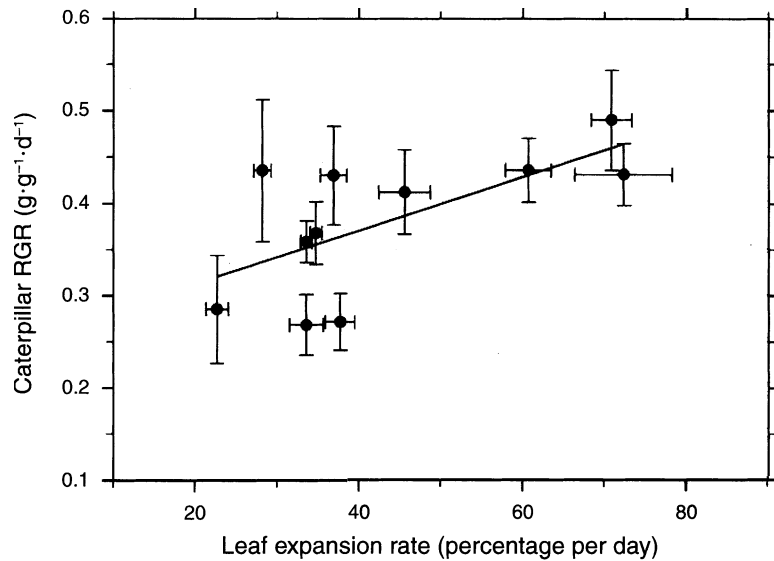


FIG. 2. Correlations between expansion rates of young leaves (%/d) for 11 species of *Inga* and the average growth rates ( $\text{g}\cdot\text{g}^{-1}\cdot\text{d}^{-1}$ ) for all caterpillar species found on each host (averaged from growth rates of individual species presented in Fig. 1). Points include standard errors for both expansion and growth,  $r^2=0.34$ ,  $P=0.03$ ,  $n=11$ . *Inga* species are *I. acuminata*, *I. cocleensis*, *I. goldmanii*, *I. laurina*, *I. marginata*, *I. multijuga*, *I. nobilis*, *I. pezizifera*, *I. sapindoides*, *I. umbellifera*, and *I. vera*.

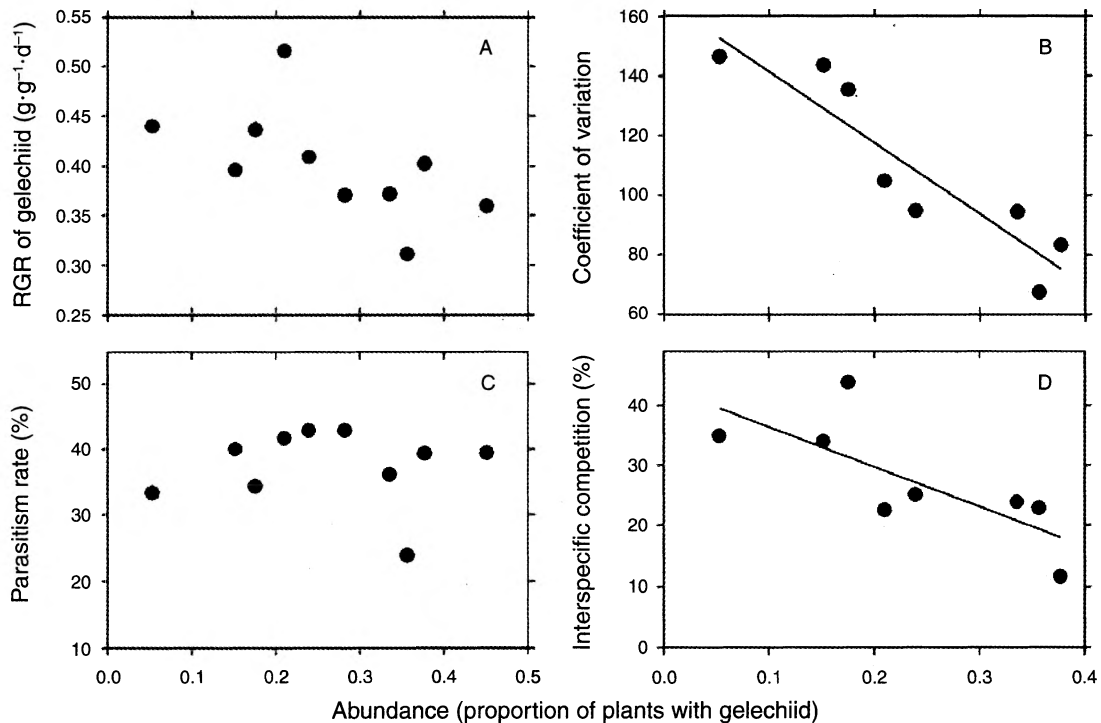


FIG. 3. The abundance of a leaf-rolling caterpillar in the family Gelechiidae in relation to growth, parasitism, competition, and resource availability. Abundance is the proportion of flushing plants that contained gelechiids. (A) Relative growth rates ( $\text{g}\cdot\text{g}^{-1}\cdot\text{d}^{-1}$ ) were measured in the lab for caterpillars reared on young leaves of the host on which they were found in the field ( $r^2=0.28$ ,  $P < 0.07$ ,  $n=10$ ). (B) The availability of food resources was measured as the synchrony of young leaf production (coefficient of variation for the percentage of plants flushing young leaves, across months). Higher values of the cv indicate greater synchrony; lower values indicate more continuous flushing ( $r^2=0.81$ ,  $P < 0.002$ ,  $n=8$ ). (C) Rates of parasitism were the percentage of individuals parasitized for 157 laboratory-reared caterpillars reared that either emerged successfully or were parasitized. Other caterpillars died of unknown causes. The relationship with abundance was not significant (ns,  $n=10$ ). (D) Interspecific competition was measured as the percentage of leaf area removed by herbivores or pathogens outside of the study while leaves were young ( $r^2=0.51$ ,  $P < 0.03$ ,  $n=8$ ).

each host. This index of competition was negatively correlated with abundance (Fig. 3D;  $r^2 = 0.51$ ,  $P = 0.028$ ,  $n = 8$ ). Competition was positively correlated with both flushing synchrony ( $r^2 = 0.76$ ,  $P < 0.02$ ,  $n = 9$ ) and expansion rate ( $r^2 = 0.69$ ,  $P < 0.04$ ,  $n = 9$ ).

We evaluated how the leaf roller's host use was affected by the combination of growth, parasitism, competition, and flushing synchrony in a multiple regression. The best fit model explained 84% of the variation in abundance ( $r^2 = 0.84$ ,  $P < 0.05$ ,  $n = 8$ ) and included parasitism, competition, and the cv of leaf flushing, all of which had negative effects on abundance in the multiple regression. The standardized regression coefficients were 0.004, 0.56, and 0.55, respectively.

#### DISCUSSION

Most lepidopteran species were found on several *Inga*, although there were definite preferences and differences in the degree of specialization. Some species were found only on one host while one species occurred on 10 hosts (Table 1, Appendix B). Even though sample sizes for individual herbivore groups were relatively small, most were found on several host species, a pattern typical of tropical herbivores (Barone 1998, Novotny et al. 2002, Novotny and Basset 2005). More extensive sampling would undoubtedly show even greater diet breadth.

Is host use related to caterpillar performance? Our data suggest that secondary metabolites have a substantial impact on growth of nonadapted herbivores. When switched to nonhosts, young-leaf feeders always grew more slowly, even if nitrogen content was adequate (Table 2). For the gelechiid, the most generalized of the *Inga* feeders, growth was 10 times slower on *I. acuminata*, a species on which the gelechiid was almost never found (electivity = 0.7%, Table 1). *Inga acuminata* is the only *Inga* known to accumulate the secondary metabolite djenkolic acid (J. Lokvam and T. A. Kursar, unpublished data). However, several species grew well on *I. acuminata* (Fig. 1), implying that chemical barriers are not universally effective. Growth differences could result from reduced consumption, greater toxicity, or metabolic load associated with detoxification (Krieger et al. 1971, Appel and Martin 1992, Berenbaum and Zangerl 1994), though our experiments did not distinguish between these possibilities. Some growth reduction occurred in five of the seven cases when caterpillars were switched to a host from which they had been recorded. Switching diets also increased mortality, but rates were similar when caterpillars were switched to normal and nonhosts. Reduced performance after switching could be due to acclimation for a specific diet or perhaps to genetic variation in performance that is linked to oviposition preference.

Furthermore, growth on mature leaves was nearly 40% slower than on young leaves, presumably because mature leaves have more fiber and less protein (Coley 1983, Marquis and Braker 1994). Perhaps as a consequence of the poor food quality of mature leaves,



PLATE 1. Expanding leaflet of *Inga umbellifera* with delayed chloroplast development (note the contrast with the mature, dark leaflets below). Ants (*Ectatomma* sp.) attracted to nectar-producing glands on the leaf rachis (not shown) tend to attract riodinid caterpillars (probably *Nymphidium* sp.). Although at least 16 species of caterpillars in the Lycaenidae and Riodinidae feed on *Inga* on Barro Colorado Island, Panama, these do not cause substantial damage. In contrast, field observations in the PDBFF study area north of Manaus, Brazil, suggest that the damage caused by caterpillars in these two families may be much greater. Photo credit: Kathleen Rudolph and Keryn Bromberg.

only 4% of the caterpillars collected were found on mature leaves. A secondary consequence of slow growth on mature leaves might be increased susceptibility to natural enemies (Benrey and Denno 1997). Thus the greater preference for young leaves and the reduced growth on nonhosts are consistent with the hypothesis that performance and preference are correlated.

Considering only young-leaf feeders and the hosts on which they are normally found, we still detected large differences in growth among different hosts. For young leaves, growth varied fivefold across all caterpillar–host combinations and fourfold among different caterpillar species feeding on young leaves of the same host (see *I. peizifera* and *marginata* in Fig. 1). In another study on BCI of 89 lepidopterans collected from 39 species of host plants in 24 families, we found sixfold variation in growth rates on young leaves (Coley et al., *in press*). Hence, variation within the *Inga* feeders approaches that found for the entire community.

As we predicted, there was a positive relationship between average growth rates of caterpillars feeding on a particular host and the rate of expansion of young leaves (Fig. 2). Young leaves with more rapid expansion have higher nitrogen and water contents, and less effective secondary metabolites (Kursar and Coley 2003). Thus, the effect of plant quality on caterpillar growth rates can be seen despite differences in herbivore life histories. These results suggest that not only do caterpillars differ in their abilities to detoxify defenses or use available nutrients, but also that *Inga* species differ in their suitability as food.

All else being equal, faster larval growth should lead to higher fitness, as faster growers can reach a larger size and/or be exposed to natural enemies for a shorter time (Lindroth and Bloomer 1991, Benrey and Denno 1997). Thus, we predicted that caterpillars should be more abundant on hosts that support faster growth. However, for the eight most common caterpillar species, there was no clear pattern of faster growth on preferred hosts (Table 2). For the gelechiid, there was a 1.7-fold difference in larval growth rates across normal hosts, but growth rate was not correlated with preference. In fact, there was a trend for lower growth rates on the most preferred hosts (Fig. 3A). Hence, all of the data on growth rates suggest that other factors were overriding, or at least modulating, the benefits of faster growth.

Other factors besides growth rates that could influence diet choice are differences among hosts with respect to rates of parasitism/predation, interspecific competition, or availability of suitable food (Crawley 1983, Ohgushi 2005). Although the availability of suitable food may be the least studied of these factors, we suggest that it could be quite important. All the *Inga* species are common, but some species produce leaves highly synchronously, making them an ephemeral food source. The gelechiid was more abundant on the species with more continuous and therefore predictable leaf production (Fig. 3B). In a study on BCI of 25 species in 14 families, synchronous leaf production was associated with rapid expansion ( $r^2 = 0.36$ ,  $P < 0.001$ ; Coley and Kursar 1996), however, within *Inga* the relationship was not significant. Thus, it appears that the gelechiid responds more to the phenology of young-leaf production than rapid expansion or associated traits (e.g., high N and low chemical defense).

Episodic leaf production is well characterized in the tropics (Aide 1988, Wright and Van Schaik 1994), and could present a widespread challenge for herbivores, the majority of which are young-leaf feeders. Other studies have also suggested that it may be difficult for herbivores to track periodic or unpredictable leaf flushing (Wolda 1988, Hunter 1992, Janzen 1993, Lawrence et al. 1997, Morais et al. 1999, Martel and Kause 2002). The mechanisms underlying this effect are not known, but a univoltine life history, diapause, or short adult life span might all contribute to the difficulty of tracking ephemeral food resources (Denlinger 1986, DeVries 1987, Janzen 1987). Thus, the evolution of the capacity to track the timing of leaf production may present a barrier to host switching (in addition to the commonly recognized factors, adaptation to toxins and oviposition preferences). Furthermore, the rhythms of leaf production and the patterns of diet choice by herbivores may influence the abundance, seasonality, and yearly fluctuations of the herbivore community (Hunter 1992, Martel and Kause 2002).

Susceptibility to the third trophic level can vary across hosts and has been suggested as a factor that influences diet selection by herbivores (Bernays 1989, Barbosa et

al. 2001, Lill et al. 2002, Singer and Stireman 2005). For example, host use by leaf beetles (Ballabeni et al. 2001), butterflies (Murphy 2004), and pine sawflies (Bjorkman et al. 1997) was associated with predator avoidance but not with physiological performance. Although parasitism rates for the gelechiid were high (24–43%), we found no differences among hosts. There was also no evidence that caterpillars could escape parasitism through fast growth or unpredictability, as there was no correlation between parasitism rates and the relative growth rate of caterpillars ( $r^2 = 0.19$ ,  $P = 0.23$ ,  $n = 10$ ), expansion rate of young leaves ( $r^2 = 0.01$ ,  $P = 0.84$ ,  $n = 10$ ), or flushing synchrony ( $r^2 = 0.05$ ,  $P = 0.58$ ,  $n = 8$ ). Although the slow growth–high mortality hypothesis has support (e.g., Häggström and Larsson 1995, Benrey and Denno 1997), this study joins several others in failing to find a relationship (Lill and Marquis 2001, Medina et al. 2005).

We did not measure predation directly, but we did measure ant visitation during the day to the extrafloral nectaries on the young *Inga* leaves (Coley et al. 2005). We found no correlation between the abundance of the gelechiid on a host species and the number of aggressive ants patrolling per square meter of leaf area ( $r^2 = 0.04$ ,  $P = 0.6$ ,  $n = 9$  host species). This suggests that leaf rolls constructed by the larvae may be effective against ants such that ant presence is not a strong negative selective factor. In addition, the five most preferred hosts have trichomes, and, as the caterpillars can walk between the trichomes, perhaps they receive additional protection against predators or parasitoids.

While Denno et al. (1995) emphasized the importance of competition, they found that leaf-feeding herbivores may experience less competition than other phytophages. Using our measure of competition, the percentage of the leaf lost to other herbivores, we found that lepidopterans that feed on young leaves, perhaps the majority of lepidopterans in the tropics, do compete. The gelechiid was significantly more abundant on hosts with less competition (Fig. 3D). Other studies have shown evidence of early-season feeders reducing leaf quality for late-season feeders (Denno et al. 2000), but in our study, competition occurred within the short 1–3 week period of leaf expansion. Furthermore, our index of competition was positively correlated with both flushing synchrony and expansion rate, suggesting that the more ephemeral the food, the higher would be the competition.

With the leaf area lost ranging from 20 to 40% during expansion, the high damage rate to young leaves suggests that direct competition for resources may be important. Nevertheless, not all the leaf tissue was removed, and competition among folivorous herbivores may often be mediated through induced defenses (Karban and Baldwin 1997, Ohgushi 2005). Damage could reduce food quality if there is induction of secondary metabolites (Haukioja and Niemelä 1979, Faeth 1986) or could increase visibility to predators if leaves with more damage give off stronger volatile or

visual signals for natural enemies (Turlings and Wäckers 2004). We are not aware of studies showing induced defenses during leaf expansion. We propose that young leaves are a limiting resource for tropical herbivores due to the combination of high damage rates and sporadic leaf production, with the role of induced defenses being unknown. Therefore, for these herbivores, edible leaf tissue may not be an abundant resource.

Clearly herbivores are balancing many selection pressures, and host preference should reflect a compromise among them (Singer and Stireman 2005). In the case of the gelechiid, growth rates differed according to the *Inga* species, but growth rates were not correlated with their abundance on different *Inga* in the field. Furthermore, despite the substantial variation in defensive chemistry among *Inga* species (Lokvam et al. 2004, Coley et al. 2005, Lokvam and Kursar 2005, Lokvam et al. 2006), the gelechiid was physiologically capable of feeding on at least 10 different hosts. Thus, nutritional and chemical traits did not pose large barriers to diet breadth. Instead, other factors appeared more important in determining host choice. We found that the best-fit multiple regression, which included competition, parasitism, and food availability, explained a substantial portion of the variation in diet choice by the gelechiid ( $r^2 = 0.84$ ,  $P < 0.05$ ,  $n = 8$ ). Thus, our results imply that ecological interactions may be more important than food quality in the initial evolution of host choice (Murphy 2004). Nevertheless, the slow growth on nonhosts observed for other species of caterpillars suggests that diet preferences based on competition, parasitism, or food availability may be reinforced by divergence among hosts in defensive chemistry and/or by loss of the ability to tolerate particular secondary metabolites on the part of the herbivore. Differences in chemistry among species of *Inga* or the loss in an herbivore lineage of metabolite tolerance would create additional barriers to host switching and lead to a correlation between physiological performance and host use. Regardless of the actual order with which these traits change during evolution, diet choice is clearly shaped by a combination of these challenges.

#### ACKNOWLEDGMENTS

We acknowledge financial support from the National Science Foundation (DEB 0108150 and DEB 0234936 to P. D. Coley and T. A. Kursar). We thank Lindsay Higgins for providing DNA sequences for three of the herbivore species. We are grateful to the Autoridad Nacional del Ambiente of Panamá and Oris Acevedo for facilitating research in Panama and to Egbert Leigh for stimulating discussions.

#### LITERATURE CITED

- Aide, T. M. 1988. Herbivory as a selective agent on the timing of leaf production in a tropical understory community. *Nature* **336**:574–575.
- Aide, T. M., and E. C. Londoño. 1989. The effects of rapid leaf expansion on the growth and survivorship of a lepidopteran herbivore. *Oikos* **55**:66–70.
- Appel, H. M., and M. M. Martin. 1992. Significance of metabolic load in the evolution of host specificity of *Manduca sexta*. *Ecology* **73**:216–228.
- Ballabeni, P., M. Włodarczyk, and M. Rahier. 2001. Does enemy-free space for eggs contribute to a leaf beetle's oviposition preference for a nutritionally inferior host plant? *Functional Ecology* **15**:318–324.
- Barbosa, P. et al. 2001. Differential parasitism of macrolepidopteran herbivores on two deciduous tree species. *Ecology* **82**:698–704.
- Barone, J. A. 1998. Host-specificity of folivorous insects in a moist tropical forest. *Journal of Animal Ecology* **67**:400–409.
- Becerra, J. X. 1997. Insects on plants: macroevolutionary chemical trends in host use. *Science* **276**:253–256.
- Benrey, B., and R. F. Denno. 1997. The slow-growth–high-mortality hypothesis: a test using the cabbage butterfly. *Ecology* **78**:987–999.
- Berenbaum, M. R., and A. R. Zangerl. 1994. Costs of inducible defense: protein limitation, growth, and detoxification in parsnip webworms. *Ecology* **75**:2311–2317.
- Bernays, E. A. 1989. Host range in phytophagous insects: the potential role of generalist predators. *Evolutionary Ecology* **3**:299–311.
- Bezzarides, A., T-H Yong, J. Bezzarides, J. Husseini, J. Ladau, M. Eisner, and T. Eisner. 2004. Plant-derived pyrrolizidine alkaloid protects eggs of a moth (*Utetheisa ornatrix*) against a parasitoid wasp (*Trichogramma ostriniae*). *Proceedings of the National Academy of Sciences (USA)* **101**:9029–9032.
- Bjorkman, C., S. Larsson, and R. Bommarco. 1997. Oviposition preferences in pine sawflies: a trade-off between larval growth and defence against natural enemies. *Oikos* **79**:45–52.
- Brenes-Arguedas, T., M. W. Horton, P. D. Coley, J. Lokvam, R. A. Waddell, B. E. O'Meara, and T. A. Kursar. 2006. Contrasting mechanisms of secondary metabolite accumulation during leaf development in two tropical tree species with different leaf expansion strategies. *Oecologia*, *in press*.
- Coley, P. D. 1983. Herbivory and defense characteristics of tree species in a lowland tropical forest. *Ecological Monographs* **53**:209–233.
- Coley, P. D., and J. A. Barone. 1996. Herbivory and plant defenses in tropical forests. *Annual Review of Ecology and Systematics* **27**:305–335.
- Coley, P. D., M. L. Bateman, and T. A. Kursar. 2006. The effects of plant quality on caterpillar growth and defense against natural enemies. *Oikos*, *in press*.
- Coley, P. D., and T. A. Kursar. 1996. Anti-herbivore defenses of young tropical leaves: physiological constraints and ecological tradeoffs. Pages 305–336 in S. S. Mulkey, R. Chazdon, and A. P. Smith, editors. *Tropical forest plant ecophysiology*. Chapman and Hall, New York, New York, USA.
- Coley, P. D. et al. 2005. Divergent defensive strategies of young leaves in two species of *Inga*. *Ecology* **86**:2633–2643.
- Colwell, R. K. 2005. EstimateS: statistical estimation of species richness and shared species from samples. Version 7.5. Department of Ecology and Evolutionary Biology, University of Connecticut, Storrs, Connecticut, USA. (<http://purl.oclc.org/estimates>)
- Crawley, M. J. 1983. *Herbivory: the dynamics of animal-plant interactions*. University of California Press, Berkeley, California.
- Croat, T. B. 1978. *The flora of Barro Colorado Island*. Stanford University Press, Palo Alto, California, USA.
- Denlinger, D. L. 1986. Dormancy in tropical insects. *Annual Review of Entomology* **31**:239–264.
- Denno, R. F., M. S. McClure, and J. R. Ott. 1995. Interspecific interactions in phytophagous insects: competition reexamined and resurrected. *Annual Review of Entomology* **40**:297–331.
- Denno, R. F., M. A. Peterson, C. Gratton, J. Cheng, G. A. Langellotto, A. F. Huberty, and D. L. Finke. 2000. Feeding-induced changes in plant quality mediate interspecific competition between sap-feeding herbivores. *Ecology* **81**:1814–1827.

- DeVries, P. J. 1987. The butterflies of Costa Rica and their natural history: Papilionidae, Pieridae, Nymphalidae. Princeton University Press, New York, New York, USA.
- Ehrlich, P. R., and P. H. Raven. 1964. Butterflies and plants: a study in plant coevolution. *Evolution* **18**:586–608.
- Faeth, S. H. 1986. Indirect interactions between temporally separated herbivores mediated by the host plant. *Ecology* **67**:479–494.
- Hägström, H., and S. Larsson. 1995. Slow larval growth on a suboptimal willow results in high predation mortality in the leaf beetle *Galerucella lineola*. *Oecologia* **104**:308–315.
- Harrison, S., and R. Karban. 1986. Effects of an early-season folivorous moth on the success of a later season species, mediated by a change in the quality of the shared host, *Lupinus arboreus* Sims. *Oecologia* **69**:354–359.
- Hassell, M. P., and T. R. E. Southwood. 1978. Foraging strategies of insects. *Annual Review of Ecology and Systematics* **9**:75–98.
- Haukioja, E., and P. Niemelä. 1979. Birch leaves as a resource for herbivores: seasonal occurrence of increased resistance in foliage after mechanical damage of adjacent leaves. *Oecologia* **39**:151–159.
- Hebert, P. D. N., A. Cywinska, S. L. Ball, and J. R. deWaard. 2003. Biological identifications through DNA barcodes. *Proceedings of the Royal Society of London, Series B*. **270**:313–321.
- Holdridge, L., W. Grenke, W. Hatheway, T. Liang, and J. Tosi. 1971. Forest environments in tropical life zones. Pergamon, New York, New York, USA.
- Holton, M. K., R. L. Lindroth, and E. V. Nordheim. 2003. Foliar quality influences tree-herbivore-parasitoid interactions: effects of elevated CO<sub>2</sub>, O<sub>3</sub>, and plant genotype. *Oecologia* **137**:233–244.
- Hunter, M. D. 1992. A variable insect-plant interaction: the relationship between tree budburst phenology and population levels of insect herbivores among trees. *Ecological Entomology* **17**:91–95.
- Janzen, D. H. 1987. How moths pass the dry season in a Costa Rican dry forest. *Insect Science and Its Application* **8**:489–500.
- Janzen, D. H. 1988. Ecological characterization of a Costa Rican dry forest caterpillar fauna. *Biotropica* **20**:120–135.
- Janzen, D. H. 1993. Caterpillar seasonality in a Costa Rican dry forest. Pages 448–477 in N. E. Stamp and T. M. Casey, editors. *Caterpillars: ecological and evolutionary constraints on foraging*. Chapman and Hall, New York, New York, USA.
- Karban, R., and I. Baldwin. 1997. Induced responses to herbivory. University of Chicago Press, Chicago, Illinois, USA.
- Krieger, R. I., P. P. Feeny, and C. F. Wilkinson. 1971. Detoxification enzymes in the guts of caterpillars: an evolutionary answer to plant defenses? *Science* **172**:579–581.
- Kursar, T. A., and P. D. Coley. 1991. Nitrogen content and expansion rate of young leaves of rainforest species: implications for herbivory. *Biotropica* **123**:141–150.
- Kursar, T. A., and P. D. Coley. 1992a. The consequences of delayed greening during leaf development for light absorption and light use efficiency. *Plant, Cell, and Environment* **15**:901–909.
- Kursar, T. A., and P. D. Coley. 1992b. Delayed development of the photosynthetic apparatus in tropical rainforest species. *Functional Ecology* **6**:411–422.
- Kursar, T. A., and P. D. Coley. 1992c. Delayed greening in tropical leaves: an anti-herbivore defense? *Biotropica* **24**:256–262.
- Kursar, T. A., and P. D. Coley. 2003. Convergence in defense syndromes of young leaves in tropical rainforests. *Biochemical Systematics and Ecology* **21**:929–949.
- Lavin, M. 2006. Floristic and geographic stability of discontinuous seasonally dry tropical forests explains patterns of plant phylogeny and endemism. In R. T. Pennington, G. P. Lewis, and J. A. Ratter, editors. *Neotropical savannas and dry forests: diversity, biogeography, and conservation*. CRC Press, Boca Raton, Florida, USA, *in press*.
- Lawrence, R. K., W. J. Mattson, and R. A. Haack. 1997. White spruce and the spruce budworm: defining the phenological window of susceptibility. *Canadian Entomologist* **129**:291–318.
- Leigh, E. G. 1999. *Tropical forest ecology: a view from Barro Colorado Island*. Oxford University Press, New York, New York, USA.
- Lill, J. T., and R. J. Marquis. 2001. The effects of leaf quality on herbivore performance and attack from natural enemies. *Oecologia* **126**:418–428.
- Lill, J. T., R. J. Marquis, and R. E. Ricklefs. 2002. Host plants influence parasitism of forest caterpillars. *Nature* **417**:170–173.
- Lindroth, R. L., and M. S. Bloomer. 1991. Biochemical ecology of the forest tent caterpillar: responses to dietary protein and phenolic glycosides. *Oecologia* **86**:408–413.
- Lokvam, J., T. Brenes-Arguedas, J. S. Lee, P. D. Coley, and T. A. Kursar. 2006. Allelochemic function in a primary metabolite: the case of L-tyrosine hyper-production in *Inga umbellifera* (Fabaceae). *American Journal of Botany*, *in press*.
- Lokvam, J., P. D. Coley, and T. A. Kursar. 2004. Cinnamoyl glucosides of catechin and dimeric procyanidins from young leaves of *Inga umbellifera* (Fabaceae). *Phytochemistry* **65**:351–358.
- Lokvam, J., and T. A. Kursar. 2005. Divergence in structure and activity of phenolic defenses in young leaves of two co-occurring *Inga* species. *Journal of Chemical Ecology* **31**:2563–2580.
- Marquis, R. J., and H. E. Braker. 1994. Plant-herbivore interactions: diversity, specificity and impact. Pages 261–281 in L. A. McDade, K. S. Bawa, H. A. Hespenheide, and G. S. Hartshorn, editors. *La Selva, ecology and natural history of a neotropical rain forest*. University of Chicago Press, Chicago, Illinois, USA.
- Martel, J., and A. Kause. 2002. The phenological window of opportunity for early-season birch sawflies. *Ecological Entomology* **27**:302–307.
- Mattson, W. J. 1980. Herbivory in relation to plant nitrogen content. *Annual Review of Ecology and Systematics* **11**:119–161.
- Medina, R. F., P. Barbosa, and K. Waddell. 2005. Parasitism levels in *Orgyia leucostigma* feeding on two tree species: implications for the slow-growth-high-mortality hypothesis. *Entomologia Experimentalis et Applicata* **115**:193–197.
- Morais, H. C., I. R. Diniz, and D. M. S. Silva. 1999. Caterpillar seasonality in a central Brazilian cerrado. *Revista de Biologia Tropical* **47**:1025–1034.
- Murphy, S. M. 2004. Enemy-free space maintains swallowtail butterfly host shift. *Proceedings of the National Academy of Sciences (USA)* **101**:18048–18052.
- Novotny, V., and Y. Bassett. 2005. Host specificity of insect herbivores in tropical forests. *Proceedings of the Royal Society of London, Series B* **272**:1083–1090.
- Novotny, V., Y. Basset, S. E. Miller, R. Kitching, M. Laidlaw, P. Drozd, and L. Cizek. 2004. Local species richness of leaf-chewing insects feeding on woody plants from one hectare of a lowland rainforest. *Conservation Biology* **18**:227–237.
- Novotny, V., S. E. Miller, Y. Basset, L. Cizek, P. Drozd, K. Darrow, and J. Leps. 2002. Predictably simple: assemblages of caterpillars (Lepidoptera) feeding on rainforest trees in Papua New Guinea. *Proceedings of the Royal Society London, Series B* **269**:2337–2344.
- Ogushi, T. 2005. Indirect interaction webs: herbivore-induced effects through trait changes in plants. *Annual Review of Ecology and Systematics* **36**:81–105.

- Osier, T. L., and R. L. Lindroth. 2001. Effects of genotype, nutrient availability and defoliation on aspen phytochemistry and insect performance. *Journal of Chemical Ecology* **27**: 1289–1313.
- Osier, T. L., and R. L. Lindroth. 2004. Long-term effects of defoliation on quaking aspen in relation to genotype and nutrient availability: plant growth, phytochemistry, and insect performance. *Oecologia* **139**:55–65.
- Pennington, T. D. 1997. The genus *Inga*. Royal Botanic Gardens, Kew Books, Cumbria, UK.
- Price, P. W., C. Bouton, P. Gross, B. McPherson, J. N. Thompson, and A. Weis. 1980. Interactions among three trophic levels: influences of plants on interactions between insect herbivores and natural enemies. *Annual Review of Ecology and Systematics* **11**:41–65.
- Raupp, M. J., and R. F. Denno. 1983. Leaf age as a predictor of herbivore distribution and abundance. Pages 91–124 in R. F. Denno and M. S. McClure, editors. *Variable plants and herbivores in natural and managed ecosystems*. Academic Press, New York, New York, USA.
- Rauscher, M. D. 1981. Host plant selection by *Battus philenor* butterflies: the roles of predation, nutrition, and plant chemistry. *Ecological Monographs* **51**:1–20.
- Richardson, J. A., R. T. Pennington, T. D. Pennington, and P. Hollingsworth. 2001. Recent and rapid diversification of a species-rich genus of neotropical trees. *Science* **293**:2232–2245.
- SAS Institute Inc. 1999–2000. Release 8.1. SAS Institute Inc., Cary, North Carolina, USA.
- Scriber, J. M., and F. J. Slansky. 1981. The nutritional ecology of immature insects. *Annual Review of Entomology* **26**:183–211.
- Singer, M. C. 2000. Reducing ambiguity in describing plant-insect interactions: “preference,” “acceptability,” and “electivity.” *Ecology Letters* **3**:159–162.
- Singer, M. S., and J. O. Stireman III. 2003. Does anti-parasitoid defense explain host-plant selection by a polyphagous caterpillar? *Oikos* **100**:554–562.
- Singer, M. S., and J. O. Stireman III. 2005. The tri-trophic niche concept and adaptive radiation of phytophagous insects. *Ecology Letters* **8**:1247–1255.
- Strong, D. R., J. H. Lawton, and R. Southwood. 1984. *Insects on plants: community patterns and mechanisms*. Blackwell Scientific, London, UK.
- Turlings, T. C. J., and F. L. Wäckers. 2004. Recruitment of predators and parasitoids by herbivore-damaged plants. Pages 21–75 in R. T. Cardé and J. Millar, editors. *Advances in insect ecology*. Cambridge University Press, Cambridge, UK.
- Viswanathan, D. V., A. J. T. Narwani, and J. S. Thaler. 2005. Specificity in induced plant responses shapes patterns of herbivore occurrence on *Solanum dulcamara*. *Ecology* **86**: 886–896.
- Wolda, H. 1988. Insect seasonality: why? *Annual Review of Ecology and Systematics* **19**:1–18.
- Wright, S. J., and C. P. Van Schaik. 1994. Light and the phenology of tropical trees. *American Naturalist* **143**:192–199.

#### APPENDIX A

A table listing the herbivore abbreviations used in the figures and tables, the morphospecies code from our database, and the scientific names (when available) of herbivores involved in the study (*Ecological Archives* E087-184-A1).

#### APPENDIX B

A figure showing the number of caterpillar species collected on different numbers of *Inga* hosts (*Ecological Archives* E087-184-A2).