POPULATION ECOLOGY - ORIGINAL RESEARCH

Do the antiherbivore traits of expanding leaves in the Neotropical tree *Inga paraensis* (Fabaceae) vary with light availability?

G. Sinimbu · P. D. Coley · M. R. Lemes · J. Lokvam · T. A. Kursar

Abstract Treefall gaps in tropical forests have a profound effect on plants growing in the understory, primarily due to increased light availability. In higher light, mature leaves typically have increased anti-herbivore defenses. However, since the majority of herbivory occurs while leaves are expanding, it is important to determine whether defense expression during the short period of leaf expansion is canalized (invariant) or plastic in response to variation in light. Therefore, we examined young leaves of *Inga paraensis* (Fabaceae) saplings growing along a light gradient in a terra-firme forest in Central Amazonia. We quantified leaf production and expansion time, dry mass of phenolics, saponins, and nitrogen, ants attracted to extrafloral nectaries, and leaf consumption. Over the entire light gradient, the number of leaves produced per flush increased by 50 % and the mass of phenolic compounds by 20 %, but no other traits changed. On average, 39 % of leaf area was consumed with no difference across the light gradient. Alone, none of the leaf traits was a significant predictor of leaf consumption, except for phenolics, which showed a positive relationship. Multiple regressions showed that leaf consumption was positively related to more leaves per flush and a higher concentration of phenolics in leaves. Unlike studies of mature leaves, young leaves of *I. paraensis* show low plasticity in defense traits across a light gradient, suggesting that leaf development is canalized.

Keywords Young leaves · Phenolics · Saponins · Canalization · Amazonia

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Introduction

Light is a limiting resource in tropical forest understories. Typically, the shaded understory receives only 1–2 % of the total photosynthetic photon flux density incident on the canopy (Chazdon and Fetcher 1984). The availability of this essential resource is increased following tree fall and gap formation, profoundly influencing forest dynamics, species interactions, and community composition. The increased light in gaps can also have direct effects on many leaf traits, including secondary metabolites, nitrogen concentration, and sugar rewards that attract defensive ants (McKey et al. 1978; Nichols-Orians 1991; Folgarait and Davidson 1994; Baraza et al. 2004).

Plastic shifts in traits in response to light have been observed in mature leaves and shown to impact the interactions between a plant, its herbivores, and its mutualistic ants (Nichols-Orians 1991; Folgarait and Davidson 1994; Baraza et al. 2004; Bixenmann et al. 2011). However, mature and young leaves differ significantly in their investments in defenses. In addition to the widespread pattern of lower fiber content and higher nitrogen concentration in the early stages of development (Kursar and Coley 2003), young leaves can also have higher concentrations of secondary metabolites (Brenes-Arguedas et al. 2006). Higher investment in these compounds is likely an evolutionary response to the herbivore's preference for young over mature leaves as a food source. Damage during the several weeks of leaf expansion averages nearly 70 % of the total leaf area that is consumed during what is typically a multi-year leaf lifetime (Coley and Barone 1996).

In tropical forests, we know little about how expanding leaves respond to increases in light levels, despite the fact that they are the main food resource for many herbivores. Leaf development could be highly regulated (i.e. canalized) such that there is little variation across light environments. This pattern has been reported for chloroplast development and some chemical defenses (Kursar and Coley 1992; Bixenmann 2011). Alternatively, young leaf traits could be plastic such that phenotypic expression responds to environmental gradients. Plasticity may merely be a reallocation of excess photosynthetic products (Bryant et al. 1983) and not necessarily an optimization of defense levels. Such responses have been observed for photosynthetic traits (Chazdon 1992; Valladares et al. 2000) and antiherbivore defenses of mature tropical leaves (Mole et al. 1988; Koricheva et al. 1998). The increased level of defense in high light could be adaptive if herbivory is consistently higher in gaps. Otherwise, canalized development could be a more successful strategy.

To investigate the extent of plasticity and its impacts on herbivory, we have studied young-leaf traits and leaf consumption across a natural light gradient. We focused on *Inga paraensis* (Fabaceae), a rainforest tree species, which belongs to one of the most speciose (>300 species) and locally abundant genera in the Neotropics (Pennington 1997). *I. paraensis* ranges from central and western Amazonia to the Guiana Shield (Pennington 1997), and at our study site near Manaus, Brazil, it was the most common of the ~ 35 co-occurring *Inga* species (Lima et al. 2007).

Predicted responses to light

To test whether expanding leaves have plastic defensive traits across a light gradient, or instead have canalized development, we chose traits that we know are variable in mature leaves or that have an effect on herbivory (Table 1). These traits are related to food availability (i.e. number of leaves produced per flush, and duration of the expansion period from bud to full size), leaf chemistry (i.e. concentration of phenolics, saponins, and nitrogen per leaf mass), and biotic defenses (i.e. number of ants attracted by extrafloral nectar). If young leaves mirror the plasticity observed in mature leaves, we expect traits to change across the light environment. Such a response would also be expected to influence herbivory. For instance, the number of leaves produced per flush should increase with light, resulting in a dilution of herbivore damage (Lierberman and Lieberman 1984; Aide 1993). High light could also increase the leaf expansion rate, thereby reducing the window of time in which leaves are most vulnerable to herbivores (Aide and Londoño 1989; Moles and Westoby 2000). Carbon-based defense metabolites, such as phenolics and saponins, are expected to increase in high light (Koricheva et al. 1998) and lead to reductions in herbivory (Henriksson et al. 2003; Potter and Kimmerer 1989). Mature leaves in high light usually have a higher photosynthetic capacity and nitrogen content per leaf area (Givnish 1988), which would increase herbivory (Mattson 1980). On the other hand, the nitrogen content of expanding leaves probably depends more on the rate of leaf expansion and leaf age (Kursar and Coley 1991). Finally, we expect more ants to be attracted to extrafloral nectaries (EFNs) in high-light habitats (Kersch and Fonseca 2005) due to higher sugar production (Folgarait and Davidson 1994; Bixenmann et al. 2011). If so, ants would reduce the rate of herbivory in gaps (Koptur 1984). Alternatively, if leaf development is canalized, the content of nitrogen and secondary metabolites may not vary across light environments. Rates of herbivory would then depend only on the abundance of herbivores in gaps versus understories, and not on the plasticity of defense traits.

Materials and methods

Study site

The study was conducted from October to November 2008 and May to October 2009 in a reserve in Central Amazonia (biological dynamics of forest fragments project reserve #1501 located at 2°24′S, 59°44′W) (see details in Bierregaard and Gascon 2001). The reserve is located 80 km north of Manaus, Amazonas, Brazil, and is embedded in a large expanse of "terra-firme" rainforest. The climate is tropical wet (Köppen type Am). The annual rainfall ranges from 1,900 to 3,500 mm (2,500 mm for the year 2009), with a distinct dry season from June to December. The average annual temperature is 26 °C. The study site, about

Table 1 Predicted positive (+) and negative (−) effects of increases in canopy openness on young-leaf traits and their effects on leaf area consumption

Traits	Effects of canopy openness on traits	Consequences for leaf area consumption	Mechanisms
Leaves per flush	+	−	Satiation of herbivores
Duration of leaf expansion (days)	−	−	Lower food availability
Phenolics (%)	+	−	Increased toxicity
Saponins (%)	+	−	Increased toxicity
Nitrogen (%)	+	+	Increased palatability
Ants	+	−	Increased biotic defense

800 ha, has a grid of trails at 100-m intervals, covering 3.8 × 2.4 km.

Light availability and leaf traits

During the 2009 field season, 95 *I. paraensis* saplings 1–5 m tall were marked along the grid of trails. For each of the 95 marked plants, we measured light availability as canopy openness using a digital camera (Nikon Coolpix 4500) with a fisheye lens (Nikon Fisheye Converter FC-E8). Hemispherical photographs can provide estimates of photosynthetic photon flux density over daily and seasonal timescales (Rich et al. 1993). Photographs were taken once directly above the flush of young leaves, following recommendations in Frazer et al. (2001), and analyzed for percentage of canopy openness (Frazer et al. 2000).

Young-leaf traits were measured on a subset of the 95 marked plants. To quantify the length of the expansion period, we marked all leaf buds with colored wire. When *I. paraensis* leaves start to expand, the EFN between the first pair of leaflets becomes active, producing nectar. Day 1 of expansion was the day when the first EFN was observed to be active and the final day was when the leaf was full size and had become tough. Because not all plants produced young leaves, and some were severely damaged during expansion, we obtained the length of the expansion period for 42 plants. At the end of leaf expansion, the percentage of the total leaf area consumed by chewing, mining, and galling herbivores was quantified using a transparent grid ($n = 93$).

We determined leaflet area for 48 individuals based on the size of the second pair of leaflets. For 15 individuals, a single mature leaflet per individual was dried on silica (at 26–30 °C) and five leaf punches (1.2 cm diameter) were weighed to determine mass per area.

During the leaf expansion period, each plant was visited twice (on average) between 0800 and 1500 hours (222 observations). We counted the ants present on young leaves (number per active EFN) and averaged values across visits per individual plant ($n = 73$).

We sampled all leaves at 80 % of full size. Because changes in metabolite concentration with age are less at this stage than at younger stages, this reduces age-related variation (Brenes-Arguedas et al. 2006). Moreover, herbivory typically peaks at this stage of development (Kursar and Coley 2003). We collected leaves from 31 plants representing the entire range of light environments, and dried them in the field with silica at 26–30 °C. In Utah, leaves were ground into a fine powder (Mixer Mill 200; Retsch). We quantified the masses of phenolics and saponins following separation by analytical-scale column chromatography (detailed extraction methods in Online Resource 1). Leaf nitrogen and carbon contents and δ^{15}N and δ^{13}C ratio were determined at the SIRFER facility (University of Utah). The contents of metabolites, N and C are expressed as a percentage of leaf dry weight. Stable isotope ratios are expressed as per mil.

During the 2008 field season, before we marked the 95 focal study plants, we quantified chlorophyll content of young leaves on unmarked saplings at the same site. We did not quantify canopy openness, but instead we chose plants growing in the understory and gaps at the extremes of the light gradient. We measured chlorophyll content following Kursar and Coley (2003) for young leaves at 80 % of full size from 12 plants in each light environment.

Statistical analyses

In order to explore how the variables were associated, we used Kendall tau rank correlation between pairs of all measured variables. To address the question of how plant traits vary with light, we performed linear regressions between the percentage of canopy openness and each of the plant traits measured. To meet assumptions of normality for this analysis, the number of ants per EFN was square-root-transformed. We used Poisson regression between percentage of canopy openness and number of leaves per flush. We assessed the effects of plant size and seasonality on responses to light using analyses of covariance (ANCOVA), with height classes (plant size in meters) and month (seasonality) as covariates.

To determine if leaf consumption varied with plant traits, we used a matrix with a sample set of the 31 individual plants for which we had data on secondary

metabolites. All plants had data on herbivory and most also had data on the other traits. Missing values were replaced by the variable mean. We performed a stepwise multiple linear regression (backward selection) starting with a model that would predict leaf consumption based on five of the measured traits: (1) number of leaves per flush log-transformed; (2) number of days to full expansion; (3) percentage of phenolics; (4) percentage of saponins; and (5) percentage of nitrogen. The number of ants was excluded from this analysis because there were many species with low frequency. We applied Akaike Information Criterion (AIC) to select the most parsimonious model that would best explain our data. All analyses were performed using R software (R Development Core Team 2009).

Results

Do plant traits vary with light?

We found *I. paraensis* saplings growing under a wide range of light conditions, spanning deeply shaded understory sites (0.4 % canopy openness) to a large gap of about 1 ha (13.3 %). The average number of leaves produced per flush per plant, 3.5 ± 2.6 leaves (mean ± SD), varied with light intensity ($n = 92$; slope = 0.264; $z = 3.632$; $P < 0.001$; Fig. 1a), and did not vary with plant size (ANCOVA $F = 4.468$; $P = 0.011$). Although more leaves were produced in higher light, morphological characteristics did not vary across the gradient. For instance, neither leaf mass per area (74.60 ± 15.33 g m^{-2}; $n = 15$; slope $= -2.96 \times 10^{-6}$; $r^2 = 0.000$; $P = 0.980$) nor leaflet size for mature leaves (165.8 ± 59.16 cm^2; $n = 48$; slope = -1.458; $r^2 = 0.007$; $P = 0.576$) varied with light. Similarly, the number of days for leaves to expand to full size, which averaged 22.3 ± 3.6 days, did not vary with light ($n = 42$; slope = -0.181; $r^2 = 0.029$; $P = 0.281$; Fig. 1b). This is equivalent to a 38 ± 8.9 % increase in size per day or 2.3 ± 0.5 days to double in size. Light availability also did not correlate with young-leaf chlorophyll content ($n = 24$; $t = 0.341$; $P = 0.736$). Plants found in shaded habitats had approximately the same chlorophyll concentration, 65 ± 16 mg m^{-2} ($n = 12$), as plants growing in gaps, 68 ± 14 mg m^{-2} ($n = 12$). These are typical values for species such as *I. paraensis* that have delayed greening and fast leaf expansion (Kursar and Coley 2003).

Gravimetric, HPLC, and mass spectrometry analyses showed that *I. paraensis* is defended by two major classes of compounds: phenolics and saponins. These represented 19.7 ± 3.6 % ($n = 28$) and 7.8 ± 1.5 % of dry weight leaf mass ($n = 29$), respectively. Phenolics were represented primarily by polymeric gallo(epi)catechin-3-*O*-gallate
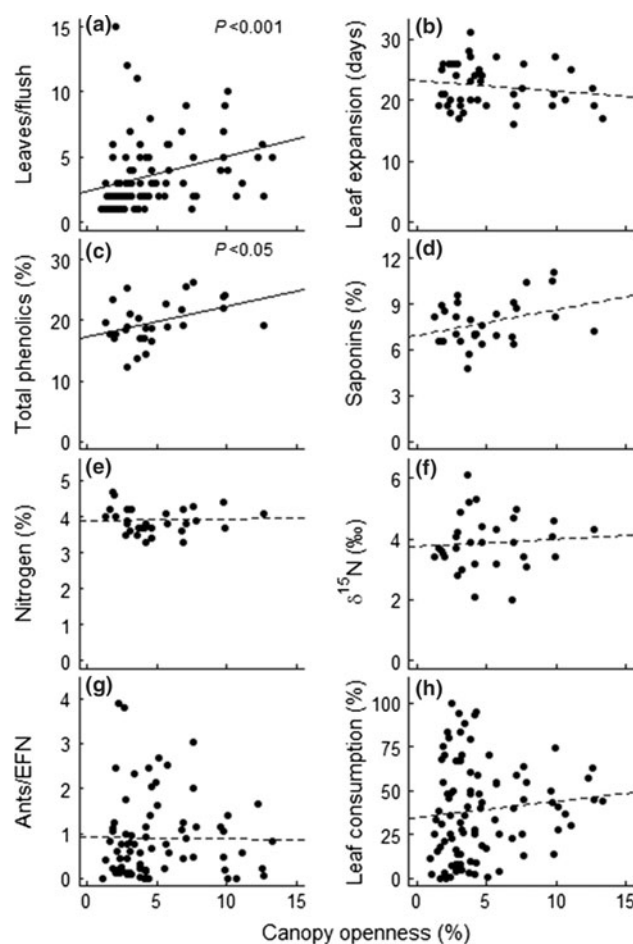

Fig. 1 The relationship between canopy openness and *Inga paraensis* young-leaf traits: **a** number of leaves per flush; **b** number of days to full leaf expansion; **c** phenolics as a percentage of leaf dry weight; **d** saponins as a percentage of leaf dry weight; **e** nitrogen as a percentage of leaf dry weight; **f** δ^{15}N per mil; **g** number of ants per extrafloral nectary; and **h** percentage of leaf area consumption. *Solid lines* represent the significant regressions ($P < 0.05$) and *dashed lines* indicate non-significant regressions

(Online Resource 1, Fig. S4a), a class of compounds widespread in the Mimosoideae and present in many *Inga* species (Lokvam, personal observation). The saponin triterpenes were mainly echinocystic and oleanolic acids (Online Resource 1, Figs. S4b and S4c). From deep shade to a large gap, the percent of the mass invested in phenolic compounds increased by 20 % ($n = 28$; slope = 0.502; $r^2 = 0.172$; $P = 0.028$; Fig. 1c), but saponins showed no change ($n = 29$; slope = 0.166; $r^2 = 0.107$; $P = 0.083$; Fig. 1d). The increase in phenolics correlated with a 21 % increase in saponins (Table 2). The phenolic:saponin ratio (2.5 ± 0.4) was constant across the light gradient ($n = 27$; slope = 0.009; $r^2 = 0.004$; $P = 0.749$).

Nitrogen content (mean = 3.9 ± 0.4 %; $n = 31$) did not vary with light (slope = 0.005; $r^2 = 0.002$; $P = 0.833$; Fig. 1e) nor did carbon content (mean = 49.4 ± 0.5 %;

Table 2 Rank correlations between pairs of leaf traits of *Inga paraensis* young leaves

r_k	Leaves per flush (92)	Leaf expansion (42)	Ants/EFN (73)	Phenolics (28)	Saponins (29)	Nitrogen (31)	δ^{15}N (31)	Leaf area consumption (93)
Canopy openness (%)	0.461***	−0.079	−0.317	0.310*	0.127	−0.017	0.271	0.092
Leaves per flush	–	−0.122	−0.124	0.418*	0.135	−0.127	0.451	0.401
Leaf expansion (days)		–	−0.009	0.018	0.080	−0.136	−0.332	0.053
Ants per EFN			–	0.142	0.295	0.274	−0.034	0.075
Total phenolics (%)				–	0.458**	0.292	0.230	0.420*
Saponins (%)					–	0.494**	−0.043	0.034
Nitrogen (%)						–	−0.130	−0.129
δ^{15}N (‰)							–	0.247
Leaf area consumption (%)								–

Values are Kendall tau coefficients. Numbers in parentheses after the column titles indicate sample size

Significance levels: * $P < 0.050$; ** $P < 0.010$; *** $P < 0.001$

$n = 31$; slope $= 0.019$; $r^2 = 0.013$; $P = 0.548$). Leaf nitrogen was positively correlated with saponin content ($r_k = 0.494$; $P = 0.001$; Table 2). The δ^{15}N values, 3.9 ± 0.9 ‰, do not classify *I. paraensis* saplings as nitrogen fixers and δ^{15}N did not vary with light ($n = 31$; slope $= 0.021$; $r^2 = 0.005$; $P = 0.715$; Fig. 1f). Although the δ^{13}C content of mature leaves typically is higher in high light, we found no variation with light (-34.4 ± 1.5 ‰; $n = 31$; slope $= 0.133$; $r^2 = 0.065$; $P = 0.166$).

We found 30 species of ants visiting the EFNs on *I. paraensis* (Online Resource 2), and 20 species were observed at least twice. *Crematogaster* spp. were the most frequent visitors representing almost 50 % of the observations. *Crematogaster* spp., as is the case for the great majority of the species observed (77 %), recruit nestmates to a resource. However, *Ectatomma tuberculatum* and *Odontomachus haematodus*, which were also common, are not group foragers. On average, we found 7.8 ± 8.3 ants per plant and 0.9 ± 0.9 ants per EFN. The number of ants per EFN did not vary with light ($n = 73$; slope $= -0.001$; $r^2 < 0.001$; $P = 0.953$; Fig. 1g).

Does leaf area consumption correlate with plant traits?

Herbivory averaged 39 ± 26.5 % and ranged from 0 to 100 % of leaf area consumed and showed no relationship to either seasonality (ANCOVA $F = 1.33$; $P = 0.246$) or plant size (ANCOVA $F = 1.406$; $P = 0.262$). The percentage of canopy openness did not predict the percentage of leaf area consumed ($n = 93$; slope $= 0.919$; $r^2 = 0.011$; $P = 0.319$; Fig. 1h). Alone, none of the leaf traits was a significant predictor of leaf consumption (Fig. 2), except for phenolics, which showed a positive relationship ($n = 28$; slope $= 3.181$; $r^2 = 0.225$; $P = 0.014$; Fig. 2e). In multiple regressions, the model which combined the log-number of leaves per flush and the percentage of phenolics best explained leaf area consumption ($R^2 = 0.327$; $P = 0.004$; AIC $= 82.67$; Table 3).

Discussion

Relative to mature leaves, our results suggest that expanding leaves showed little trait plasticity in response to light. In our study, none of the leaf traits varied with light except for a 20 % increase in the mass of phenolics. On average, mature leaves of tropical plants respond to light by increasing total phenolics by 190 % and condensed tannins by 260 % (Online Resource 3). Leaf mass per area and leaflet size also showed no plasticity across the light gradient, a result consistent with data on other shade-tolerant species (Poorter et al. 2009). Minimal or complete absence of plasticity in young leaf traits suggests that leaf development is rather canalized with respect to light. A possible explanation for this is that, even though photosynthetic resources vary with light, plasticity would only be advantageous if leaf consumption were influenced by light incidence, which it is not. Thus, our results illustrate that expanding leaves of *I. paraensis* do not follow the same trend for plasticity found in mature leaf traits across light gradients (e.g., references in Online Resource 3).

Food availability

Herbivores on expanding leaves may experience food limitation due to a short window of availability as well as competition among herbivores for food (Kursar et al. 2006). As such, the number of leaves per flush and the leaf expansion rate may be a good measure of food availability to herbivores. Expansion rate did not differ across the light gradient. However, the number of leaves produced per flush increased by 50 % with light, perhaps due to more
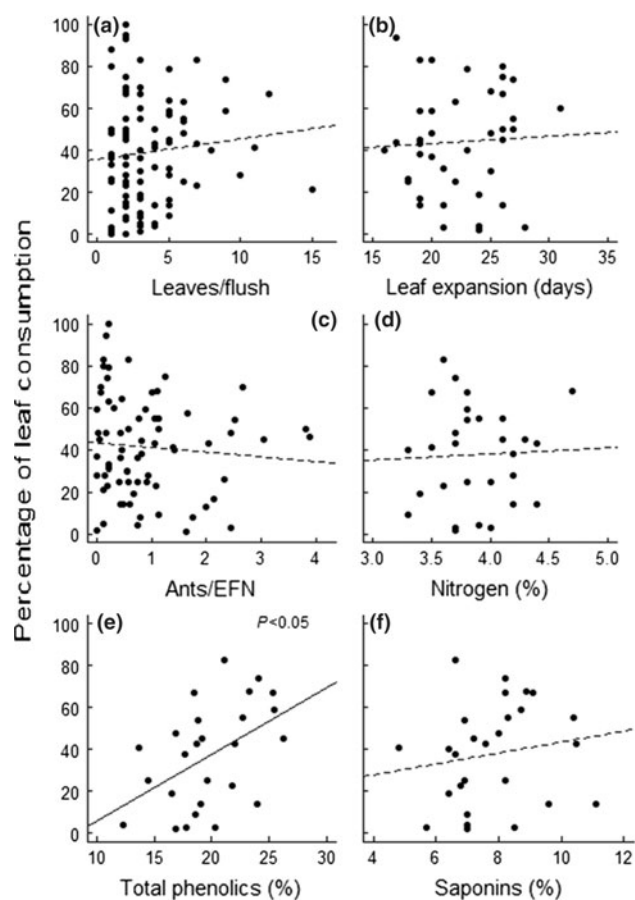
Fig. 2 The relationship between *Inga paraensis* young-leaf traits and leaf area consumption by herbivores: **a** number of leaves per lush; **b** number of days to leaf full expansion; **c** number of ants per extrafloral nectary; **d** nitrogen as a percentage of leaf dry weigh; **e** phenolics as a percentage of leaf dry weight; and **f** saponins as a percentage of leaf dry weight. *Solid lines* represent the significant regressions ($P < 0.05$) and *dashed lines* indicate non-significant regressions

photosynthesis and stored resources. Although Richards and Coley (2007) found greater food availability in gaps (i.e. more young leaves), the abundance of herbivores (including more species) also was higher. We did not find

an increase in herbivory with light, suggesting that herbivore pressure in our study site may not be different in gaps versus the understory.

Leaf chemistry

Nitrogen content was not related to increased light. This is consistent with the lack of a relationship between chlorophyll content and light in the present study and in Kursar and Coley (1992). Among defense metabolites, only the level of phenolic metabolites correlated with light availability, although increases were modest (20 %) when compared to those reported for mature leaves (Online Resource 3). To our knowledge, our study is the first to measure saponin concentration over a natural light gradient, and we found no significant variation. The Carbon-Nutrient Balance Hypothesis predicts that, since both phenolics and saponins are carbon-based compounds, their concentrations should increase with increasing photosynthesis in high-light environments where nutrient availability is limiting (Bryant et al. 1983). Results from studies on mature leaves have been consistent with this prediction (Online Resource 3), even when controlling for genetic variation (Mole et al. 1988; Henriksson et al. 2003). We suggest that young and mature leaves respond differently to light availability and that such a difference may be due to constraints during development. Young *Inga* leaves invest 40–50 % of dry weight in secondary metabolites (30 % in soluble fractions with the remainder in cell-wall-bound phenolics; Lokvam and Kursar 2005). Thus, it may be physiologically impossible to increase defense investments without compromising leaf structure and function. The initially high concentration of secondary metabolites is generally diluted as the maturing leaf lays down secondary cell walls and lignifies (Kursar and Coley 2003; Brenes-Arguedas et al. 2006). However, even in the young leaves with low investment in cell walls, it may be difficult to invest more than 50 % of the dry weight in secondary metabolites and maintain leaf growth. Hence, high constitutive investment

Table 3 Multiple regression models of percentage of leaf area consumption

Predictor variables	R^2	P	AIC
log LEAVES* + DAYEXP + PHENOLIC* + SAPONIN + NITROGEN	0.335	0.056	−1.65
log LEAVES* + DAYEXP + PHENOLIC* + SAPONIN	0.332	0.027	−3.53
log LEAVES** + PHENOLIC* + SAPONIN	0.329	0.011	−5.41
log LEAVES + PHENOLIC***	**0.327**	**0.004**	**−7.31**
log LEAVES***	0.231	0.006	−5.16

Models are ranked by complexity of predictor variables: log *LEAVES* logarithm of the number of leaves per flush; *DAYEXP* number of days to leaf full expansion; *PHENOLIC* percentage of phenolics in leaf mass; *SAPONIN* percentage of saponins in leaf mass; *NITROGEN* percentage of nitrogen in leaf mass. Correlation coefficients (R^2), P values and Akaike information criterion (AIC) values are presented for each model. Bold type indicates the best model based on AIC values

Significance levels: * $P < 0.10$; ** $P < 0.05$; *** $P < 0.01$

may constrain the capacity to increase the amount of secondary metabolites in response to higher light.

Unexpectedly, phenolic content was positively correlated with leaf consumption, although similar observations were made in other studies (Sipura and Tahvanainen 2000; Henriksson et al. 2003; Chacón and Armesto 2006). It is hypothesized that specialist herbivores adapted to feed on a given plant species may have the ability to consume phenolics and would therefore be more influenced by nutrients, such as water, proteins, and carbohydrates (Henriksson et al. 2003). For instance, Nichols-Orians (1991) found a positive correlation with leaf consumption and phenolics in a different species of *Inga* and argued that the deterrent effects of secondary metabolites were masked by a higher nutritional value. In the present study, nitrogen content did not correlate with either herbivory or phenolics (we did not measure carbohydrates). It is not clear why we find that leaf consumption correlated positively with phenolics. A positive correlation could result from induction; however, work in other *Inga* species has shown that neither phenolics nor saponins are induced by herbivores (Bixenmann 2011).

Our predictions of higher ant abundance in high-light habitats were based on studies that showed more sugar rewards (Folgarait and Davidson 1994; Bixenmann et al. 2011) and higher densities of ants in gaps (Richards and Coley 2007). We found no evidence of increased ant visitation in higher light. Since we did not determine whether there was a relationship between nectar production and light, a detailed analysis of our ant visitation results is beyond the scope of this study.

Plasticity versus canalization

It is well documented that the anti-herbivore traits of mature, sun leaves differ from shade leaves (Online resource 3), including one study from *Inga* (Nichols-Orians 1991). However, despite an approximately 33-fold range of light intensities, we have shown that the defensive traits of expanding leaves of *I. paraensis* varied little across the light gradient. One possibility is that leaf development is canalized due to constraints resulting from the complex regulatory networks inherent to development (Siegal and Bergman 2002). Alternatively, plasticity may not be advantageous. Specifically, increased defenses in higher light will only be beneficial if herbivore attack is greater in high light, and we have evidence that that is not the case in *I. paraensis*. Other studies of expanding leaves also report that leaf consumption is the same in the understory and gaps (Howlett and Davidson 2001; Eichhorn et al. 2006). Thus, although there is a strong environmental cue, phenotypic plasticity appears not to be advantageous in *I. paraensis*. Whether little plasticity during leaf expansion

is a universal pattern for tropical trees remains to be further tested.

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