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EFEITO DA LUMINOSIDADE NAS CARASTETÍSTICAS DE DEFESA CONTRA HERBÍVOROS DE *Inga paraensis* Ducke (FABACEAE: MIMOSOIDEAE)

Georgia Sinimbu Silva

Manaus, Amazonas
Abril, 2010

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Sinopse:

Estudo do efeito da variação na incidência luminosa nas características de produção e composição química de folhas em expansão e conseqüências no consumo por herbívoros, em uma Floresta na Amazônia Central. Foram avaliadas características relativas à defesa contra herbívoros em folhas em expansão, relacionadas à incidência luminosa e porcentagem de consumo foliar.

Palavras-chaves: desenvolvimento foliar, fenóis, saponinas, formigas, herbivoria, florestas tropicais, Amazônia, *Inga*.

Dedicatória

Aos meus pais
e à tia Verônica

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“*Tu deviens responsable*
pour toujours de ce que
tu as apprivoisé”
dit le renard au Petit Prince.

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Às *Inga paraensis* e todas as árvores
Às lagartas e aos besouros, em especial Paul McCartney
À você que lê
a minha reverência.


SOMETIMES I THINK THE SUREST SIGN THAT INTELLIGENT LIFE EXISTS ELSEWHERE IN THE UNIVERSE IS THAT NONE OF IT HAS TRIED TO CONTACT US.
WATTERSON

RESUMO

Efeito da luminosidade nas características de defesa contra herbívoros de *Inga paraensis* Ducke (Fabaceae: Mimosoideae)

A formação de clareiras em florestas tropicais exerce profundo efeito nas plantas que se desenvolvem no sub-bosque, especialmente devido ao aumento na disponibilidade de luz. Nós examinamos a plasticidade ambiental das características vegetais de defesa contra herbívoros, focando em folhas em expansão, fase durante a qual ocorre a maioria dos danos por herbívoros. Nós amostramos arvoretas de *Inga paraensis* ao longo de um gradiente de luz no sub-bosque de uma floresta de terra-firme na Amazônia Central. Nós quantificamos as seguintes características: produção e tempo de expansão de folhas; massa seca de fenóis totais, saponinas e nitrogênio; atração de formigas aos nectários extraflorais e consumo foliar. Modelos de regressão foram utilizados com combinações de características de folhas em expansão através de uma análise de componentes principais (ACP) para prever o consumo foliar. Nós encontramos arvoretas crescendo sob uma grande variação de condições luminosas, desde sub-bosques sombreados (com 0,4% de abertura de dossel) a grandes clareiras (com 13,3% de abertura de dossel). A intensidade de luz afetou positivamente o número de folhas produzidas durante a brotação e a massa de compostos fenólicos, porém, sem efeito sob outras características. Em média, 39% da área foliar foi consumida ao longo do gradiente de luz. A ACP revelou quatro componentes principais que explicaram 87% da variação entre plantas. Em geral, as características foram combinadas em termos de composição química das folhas e características de crescimento. Regressão linear da herbivoria enquanto função das características de desenvolvimento demonstrou que o consumo foliar foi explicado pela expansão lenta e a redução na produção de folhas durante a brotação. Assim, diferente de estudos com folhas maduras, folhas em expansão de *I. paraensis* apresentam pouca plasticidade quanto às características de defesa contra herbívoros ao longo de um gradiente de luz, sugerindo que o desenvolvimento das folhas jovens se deve a um processo fisiológico canalizado.

ABSTRACT

Light effect on antiherbivore traits of *Inga paraensis* Ducke (Fabaceae: Mimosoideae)

The formation of treefall gaps in tropical forests has a profound effect on plants growing in the understory, specifically due to increased light availability. We examined plasticity to light of antiherbivore traits, focusing on expanding leaves, the phase where the majority of herbivory occurs. We sampled *Inga paraensis* (Fabaceae) saplings along a light gradient in a *terra-firme* forest in Central Amazonia. We quantified the following traits: leaf production and expansion time; dry mass of total phenolics, saponins and nitrogen; ants attracted to extrafloral nectaries; and leaf consumption. Regression models were performed with a combination of young leaf traits by principal component analysis (PCA) as predictor to leaf consumption. We found saplings growing under a wide range of light conditions, from deeply shaded understory (0.4% canopy openness) to large gaps (13.3%). Light intensity positively affected the number of leaves produced per flush and the mass of phenolic compounds, but had no effect on any other trait. On average, 39% of leaf area was consumed with no difference across the light gradient. A PCA of leaf traits revealed four principal components that explained 87% of the variation among plants. In general, traits were combined into leaf chemical composition and traits affecting leaf growth. Linear regression of herbivory as a function of growth traits showed the leaf consumption was best explained by slow-expansion of leaves and fewer leaves produced per flush. Thus, unlike studies of mature leaves, young leaves of *I. paraensis* show remarkably little plasticity in defense traits across a light gradient, suggesting that young leaf development is due to a canalized physiological process.

SUMÁRIO

INTRODUÇÃO

0A luz é um recurso limitante no sub-bosque de florestas tropicais. Normalmente, as plantas que crescem em sub-bosque sombreado recebem apenas 1-2% da densidade total do fluxo de fótons fotossintéticos (DFFF) incidente no dossel (Chazdon e Fetcher, 1984). No entanto, processos relacionados a dinâmica florestal proporcionam aumento na disponibilidade desse recurso essencial, principalmente em função da formação de clareiras. Por exemplo, pequenas clareiras com menos de 200 m² ou pelo menos 5% de abertura do dossel aumentam em até nove vezes a DFFF (Chazdon e Fetcher, 1984; Chazdon, 1992). O papel das clareiras tem sido bastante investigado ao longo dos anos e muitos estudos registram a importância da luz alterando as condições ambientais e consequentemente as comunidades biológicas com especial atenção para a riqueza e abundância de plantas (Connell, 1979; Hubbell *et al*. 1999). Desse modo, os efeitos da variação natural da luz nos fenótipos de vegetais, ou na plasticidade fisiológica, tem recebido considerável atenção.

A plasticidade fenotípica é a mudança na expressão das características associada às variações no ambiente e que, em geral, permite que as plantas se adaptem às novas condições (Metlen *et al*., 2009). A plasticidade em relação a ambientes com maior intensidade luminosa pode afetar positivamente a capacidade de uma planta em tolerar danos por herbívoros (Maschinski e Whitman, 1989), bem como a resistência da planta a esses danos (Koricheva *et al*., 1998). Koricheva et al (1998) apresentam uma compilação de diversos estudos sobre plsticidade na resistênicia sendo que na maioria deles os quais os autores focam em folhas maduras. No entanto, em florestas tropicais, folhas em expansão são o principal recurso para os herbívoros. Danos por herbívoros durante as várias semanas de expansão foliar atingem até 80% da área foliar total que será consumida durante a vida de uma folha, um período de cerca de dois anos (Coley e Barone, 1996).

A diferença nos danos causados por herbívoros em folhas em expansão vs. maduras é atribuída às diferenças na adoção de estratégias de defesa pelas plantas. Em folhas maduras, o dano é principalmente reduzido devido à dureza da folha, enquanto que as folhas jovens apresentam uma maior variedade de mecanismos de defesa (Kursar e Coley, 2003). Estes mecanismos podem ser agrupados em duas estratégias contrastantes: "defesa" e "escape". Enquanto as espécies que se defendem reduzem a perda de folhas, através do investimento em defesas químicas, de expansão foliar lenta e da maturação dos cloroplastos durante a expansão, espécies que escapam equilibram defesas químicas menos eficazes com uma rápida expansão foliar, atraso na maturação dos cloroplastos e produção sincrônica de folhas (Kursar e Coley, 2003). A adoção dessas estratégias pelas plantas é entendida, sobretudo, em um contexto evolutivo. Portanto, é esperado que variações ambientais não conduzam a plasticidade entre as estratégias. Em vez disso, espera-se que a variação intra-específica seja uma resposta passiva aos aumentos de luz e seus efeitos sobre a fisiologia da planta (Lerdau e Coley, 2002). Assim, em comparações intra-específicas, espera-se que as características de defesa nas plantas aumentem com a disponibilidade de recursos. A exemplo disso, espera-se que compostos de defesa de base carbono aumentem com aumento na produção de carbono devido a maiores taxas fotossintéticas em ambientes enluminados (Bryant *et al.*, 1983).

OBJETIVOS

Neste estudo, nós investigamos como as diferenças na disponibilidade de luz afetam as características de defesa de folhas jovens (i.e. folhas em expansão) de *Inga paraensis* e, conseqüentemente, a herbivoria em arvoretas crescendo sob um gradiente natural de luz numa floresta situada na Amazônia Central. Especificamente, nós verificamos as respostas de *I. paraensis* a diferentes intensidades de luz, por meio da quantificação das seguintes características: produção da folha, tempo de expansão foliar, concentração de metabólitos secundários (fenólicos totais e saponinas), teor de nitrogênio, formigas atraídas para nectários extraflorais (EFN) e consumo de folhas em expansão por herbívoros. Nossa hipótese foi que se folhas jovens espelham os padrões gerais vistos em folhas maduras, as características das plantas serão plásticas e plantas em ambientes com maior intensidade de luz terão um maior investimento em defesas contra herbívoros. No entanto, se apesar da variação ambiental as plantas apresentarem pouca plasticidade, poderemos supor que o desenvolvimento da folha se deve a um processo fisiológico canalizado (i.e.

fenótipo consistente) e nós esperamos encontra pouca variação nos fenótivos das características de defesa.

Does light availability affect the antiherbivore traits of saplings of a shade-tolerant tree, *Inga paraensis*? [*]

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Abstract

The formation of treefall gaps in tropical forests has a profound effect on plants growing in the understory, specifically due to increased light availability. We examined plasticity to light of antiherbivore traits, focusing on expanding leaves, the phase where the majority of herbivory occurs. We sampled *Inga paraensis* (Fabaceae) saplings along a light gradient in a *terra-firme* forest in Central Amazonia. We quantified the following traits: leaf production and expansion time; dry mass of total phenolics, saponins and nitrogen; ants attracted to extrafloral nectaries; and leaf consumption. Regression models were performed with a combination of young leaf traits by principal component analysis (PCA) as predictor to leaf consumption. We found saplings growing under a wide range of light conditions, from deeply shaded understory (0.4% canopy openness) to large gaps (13.3%). Light intensity positively affected the number of leaves produced per flush and the mass of phenolic compounds, but had no effect on any other trait. On average, 39% of leaf area was consumed with no difference across the light gradient. A PCA of leaf traits revealed four principal components that explained 87% of the variation among plants. In general, traits were combined into leaf chemical composition and traits affecting leaf growth. Linear regression of herbivory as a function of growth traits showed the leaf consumption was best explained by slow-expansion of leaves and fewer leaves produced per flush. Thus, unlike studies of mature leaves, young leaves of *I. paraensis* show remarkably little plasticity in defense traits across a light gradient, suggesting that young leaf development is due to a canalized physiological process.

Keywords: light gradient; leaf development; phenolics; saponins; ants; herbivory; tropical rainforest; Amazonia; *Inga*

Introduction

Light is a limiting resource in tropical forest understories. Typically, plants growing in shaded understory receive only 1-2% of the total photosynthetic photon flux density (PPFD) incident on the canopy (Chazdon and Fetcher 1984). However, forest dynamic processes provide increases in the availability of this essential resource essentially by gap formation. For instance, small gaps, of less than 200 m^2 or at least 5% of canopy openness, can experience up to nine times greater PPFD than in closed canopy understory (Chazdon and Fetcher 1984, Chazdon 1992). The role of light gaps has been well explored over the years with many studies revealing the importance of light altering environmental conditions and consequently biological communities, with special regard to plant richness and abundance. Therefore, the effects of natural variation in light on plant phenotypes, or physiological plasticity, has received considerable attention.

Phenotypic plasticity is the change in the expression of traits that is associated to variation in the environment that, in general, allows plants to get adapted to the new conditions (Metlen et al 2009). Plasticity to light environments are suggested to affect positively a plant’s ability to tolerate herbivores (Maschinski and Whitman 1989), as well as plant resistance to damage by increased defenses (Koricheva et al 1998). Koricheva et al (1998) present a compilation of many studies on plasticity on resistance in which the focus has been mostly on mature leaves. However, in tropical forests, young leaves are the main resource to herbivores. Damage during several weeks of leaf expansion can equal up to 80% of the total leaf area that is consumed during the life of a leaf, a period of about two years (Coley and Barone 1996).

The difference in damage due to herbivores between young vs. mature leaves is attributed to differences in defensive strategies. For mature leaves, damage is mainly decreased by leaf toughness, whereas young leaves have a greater variety of defense mechanisms (Kursar and Coley 2003). Those mechanisms can be grouped in two contrasting strategies: ‘defense’ and ‘escape’. While defense species reduce leaf loss through investment in chemical defenses, slow leaf expansion and normally greening leaves, escape species, are predicted to balance less effective chemical defenses with rapid leaf expansion, delayed chloroplast maturation and synchronous leaf production (Kursar and Coley 2003). The adoption of these strategies by plants can mostly be understood under an evolutionary context. Therefore, environmental variations are not expected to drive plasticity among strategies. Instead, intraspecific variation is expected to be a passive response to light increases and its effects over plant physiology (Lerdau and Coley 2002). Thus, in within species comparisons, the plant defensive traits are expected to enhance with resource availability. For instance, carbon based defensive compounds are expected to enhance with carbon increases due to higher photosynthesis in light rich environments (Bryant et al 1983)

Here we ask how differences on light availability affect young leaf traits and consequently herbivory of saplings of *Inga paraensis* growing under a natural light gradient. Specifically, we examine responses to light gradient traits such as leaf production, leaf expansion time, secondary metabolite contents (total phenolics and saponins), nitrogen content, ants attracted to extrafloral nectaries (EFN), and the amount of young leaves consumed by herbivores. We hypothesized that if young leaves mirror the general patterns seen for mature leaves, plasticity will be observed in plant traits and plants in light habitats will have higher investment on antiherbivore defenses. Nonetheless, in spite of variable environmental features, plants experience little plasticity, we may assume that leaf development is canalized (i.e. phenotype consistence) and we expect to find little variation on phenotypes of defensive traits.

Predicted responses to light

To address these hypotheses, we focused on *Inga paraensis* (Fabaceae: Mimosoideae), a rainforest tree species. *Inga* is a speciose (>300 species) and locally abundant genus in Neotropics (Pennington 1997). At our study site in Central Amazonia, *I. paraensis* was the most common of the ~ 35 co-occurring *Inga* species (Coley and Kursar, personal observation) and its distribution ranges from central and western Amazonia to the Guiana Shield (Pennington 1997).

Inga species invest in a variety of defense traits, including direct antiherbivore defenses such as morphological traits (hairs and toughness) and secondary compounds that may approach 50% of the leaf dry mass (Lokvam and Kursar 2005). Moreover, *Inga,* like all species from the Mimosoideae group, has extrafloral nectaries (EFN) between leaflets pairs that act as indirect defenses. Ants are attracted by nectar production during leaf expansion and provide protection against herbivores in exchange for the sugar rewards (Koptur 1984). If young leaves of *I. paraensis* experience plasticity, we predict based on a passive response to light that defensive traits will be affected as shown in figure 1, with increased light triggering changes that reduce the herbivory damage. For instance, escape traits such as synchronous leaf production and rapid leaf expansion will increase in order to dilute herbivory damage (Lieberman and Lieberman 1984, Aide 1993) and to reduce the window of time in which leaves are suitable for consumption (Aide and Londoño 1989, Moles and Westoby 2000). Carbon-based secondary metabolites, such as total phenolics and saponins are expected to increase as light increases (Koricheva et al 1998). The majority of secondary metabolites are commonly known as antiherbivore metabolites and we expect that increases in their concentration will deter herbivores. However, leaves in high light also have a higher photosynthetic capacity as well as higher leaf nitrogen content (Givnish 1988), and higher nitrogen may enhance attractiveness to herbivores (Mattson 1980). Finally, we expect more ants to be attracted to EFN due to higher sugar production in high light habitats (Folgarait and Davidson 1994, Bixenmann et al in prep), which consequently would reduce herbivory.

Material and Methods

Study site

This study was conducted from October to November 2008 and May to October 2009 in an 800 ha reserve in Central Amazonia (Reserve Km 41 located at 2º24'S, 59º44'W) administrated by the Biological Dynamics of Forest Fragments Project (BDFFP, see study area details on Bierregaard and Gascon 2001). The reserve is located 80 km North of Manaus, Brazil), and is embedded in a large expanse of *terra-firme* rainforest. The climate is humid tropical

(Köppen type Am) with a distinct dry season from June to December, annual rainfall ranged from 1,900 – 3,500 mm and average annual temperature is 26° C. The study site has a square grid of trails at 100 m intervals, covering 3.8 x 2.4 km.

Field measurements

Inga paraensis saplings 1 to 5 m tall were marked along the trails. To characterize plant's habitat, we measured light availability as canopy openness. For each plant, a digital camera (Nikon Coolpix 4500) with a fisheye lens (Nikon Fisheye Converter FC-E8) was positioned directly above the flush of young leaves. Afterwards, the photographs were analyzed using the computer software Gap Light Analyzer (GLA, Frazer et al 1999).

In order to achieve the time necessary to complete leaf development, we quantified in days the length of the expansion period. For each plant, we marked all leaf buds with colored wire. In *I. paraensis* when leaves start to expand, the EFN between the first pair of leaflets becomes active producing nectar to attract ants. Day 1 of expansion was the day when the first EFN was observed active and final day when the leaf reached the final leaf area, turned green and became tough. At the end of leaf expansion, the percentage of the total leaf area consumed by chewing, mining, and galling herbivores was estimated visually.

In order to characterize the species, we determined young leaf chlorophyll content. We chose 12 plants in each of the extreme habitats (light and shade). For those specific individuals, habitats were defined visually; light habitat represent gaps with opened canopy understory while shaded habitat, closed canopy understory. Methodology for chlorophyll quantification followed Kursar and Coley (2003).

During leaf expansion period, plants were visited on average twice for determine the number of ants. We visited plants only during the day (between 8 AM and 3 PM) because caterpillars are as active during day period as night period (Coley, personal observation). The number of ants present in young leaves and active EFNs was counted on each visit, and all values were averaged per individual plant and per EFN. No more than one individual of each ant species per plant was collected in Eppendorf tubes with alcohol 70% for further identification provided by J. M. da S. Vilhena from CPEC/INPA. Reference specimens were housed at CPEC/INPA collection in Manaus, Brazil. Most individuals from the genus *Crematogaster*, *Pheidole* and *Solenopsis*, which were not possible to identify to lower taxonomic levels, were grouped per genus. Species frequency was calculated for two classes of habitats: shade, < 5% canopy openness, and light, ≥ 5% canopy openness. The limit adopted was based on field observations.

Leaf chemistry

We collected young leaves from 31 plants with approximately 80% of expanded area. They were dried with silica at 26-30° C under environment conditions for chemical analyses. Dried young leaves were ground into a fine powder using a Mixer Mill 200 (Retsch GmBH). The masses of total phenolics and saponins were quantified by analytical-scale column chromatography (protocol adapted for small samples from Fig S5 in Kursar et al 2009). Briefly, we placed 200 mg of ground sample into 40 ml teflon centrifuge tubes and extracted twice with 80% ethanol and twice with 70% acetone (AcO) for 15 minutes while stirring. Extracts were centrifuged at each step and the solvent was removed by pipette. Following extraction, the combined extracts (ethanol + acetone) were dried under vacuum and resuspended in methanol (MeOH – 15 ml). This solution was defatted twice in a teflon centrifuge tube with 15 ml of hexanes. The defatted methanol layer was diluted with water (15 ml) and the MeOH was removed under vacuum. The remaining aqueous solution was applied to a 2 cm x 9.5 cm column containing 4 g of octadecyl silane (JT Baker Company, 40 µm mesh size) that had been equilibrated with 5% MeOH. The solution was driven onto the column under vacuum, then the following fractions were collected: 1) 40 ml of 5% MeOH – amino/organic acids and sugars fraction; 2) 10 ml of 5% MeOH – quality control blank fraction; 3) 20 ml of 60% MeOH – flavan/flavone fraction; 4) 10 ml of 60% MeOH – a quality control, blank fraction; 5) 20 ml of 100% MeOH – saponin fraction; and 6) 20 ml of 70% AcO – a quality control, blank fraction. All fractions were dried at 25° C under vacuum and weighed. High performance liquid chromatography (HPLC) with diode array, evaporative light-scattering and mass spectrometric detection was used to verify the identity of the flavan/flavone and saponin fractions. Leaves samples were analysed at the SIRFER laboratory (University of Utah) for quantification of nitrogen and its stable isotopes.

Statistical analyses

We used a t-test to compare leaf chlorophyll content for plants found in light and shade habitats. All other analyses were performed using data in which plants were sampled along a light gradient. In order to explore how the variables were associated, we used Kendall tau rank correlation between pairs of all measured variables for all 95 plants observed with some missing variables observations.

To address the question of how light affects plant traits, 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.

To explore dissimilarities in the biological assemblage matrix relative to plants' spatial location and percentage of canopy openness (habitat), we built a matrix with presence-absence data on ant species visiting EFN from 88 plants and performed Mantel tests (1,000 permutations). Habitat and spatial dissimilarity were computed as Euclidean distances whereas dissimilarity distance in the biological matrix was calculated by Bray-Curtis index (Oksanen 2009).

To determine if plant traits affect leaf consumption we used a matrix with a sample set of 31 individual plants (whenever there was a missing values, it was replaced by the variable mean). To determine how plant traits and environment interacted to affect herbivory, we used a two-step analysis approach (adapted from Philippi 1993). First, we used principal components analysis (PCA) to identify combinations of measured variables that were inter-correlated and second we used simple regressions between the PCA axes and percentage of leaf area consumption. The PCA was performed with six variables: 1) number of leaves per flush log-transformed; 2) number of days to leaf full expansion; 3) percentage of total phenolics in leaf mass; 4) percentage of saponins in leaf mass; 5) percentage of nitrogen in leaf mass; and 6) number of ants per EFN square-root-transformed. We used the correlation matrix among variables to generate PCA scores in order to scale the units of measurements for the variables. We chose a 0.400 minimum loading coefficient to consider a given variable significant to load on a PCA axis. To test whether the percentage of leaf area consumption was predicted by combinations of the measured variables, we preformed simple linear regressions with the scores of the orthogonal principal components as predictor variables. Only the axes that would account for at least 10% of the variance among plants (eigenvalues $\geq$ 0.8) were used.

As complementary analysis, we performed a stepwise multiple linear regression using as start point for the back selection of variables a model that would predict leaf consumption based on six traits: 1) number of leaves per flush log-transformed; 2) number of days to leaf full expansion; 3) percentage of total phenolics in leaf mass; 4) percentage of saponins in leaf mass; 5) percentage of nitrogen in leaf mass; and 6) number of ants per EFN square-root-transformed. For the next model, we subtracted from the previous one the variable with the highest p-value. We applied Akaike Information Criterion (AIC) to select the most parsimonious model which would best explain our data. All analyses were performed using R software (R Development Core Team 2009).

Results

Does light affect *I. paraensis* traits?

We found *I. paraensis* saplings growing under a wide range of light conditions, spanning deeply shaded understory (0.4% canopy openness) to a large gap of about 1ha (13.3%). The average number of leaves produced per flush per plant, 3.5 ± 2.6 leaves (mean ± SD), was positively affected by light (slope=0.264; z=3.632; $p<0.001$; figure 2A). However, light did not affect the number of days for leaves to expand to full size (slope=-0.181; $R^2=0.029$; $p=0.281$; figure 2B), which averaged 22.3 ± 3.6 days. In order to allow comparisons with other studies, the average percent increase in size per day was 38 ± 8.9% per day the average number of days to double in size 2.3 ± 0.5 days. Light intensity also did not affect young leaf chlorophyll content (d.f.=21; *t*=0.341; *p*=0.736, figure 3). Plants found in shade habitats had approximately the same chlorophyll concentration, 65.4 ± 16.9 mg/dm^2 (n=12), as plants growing under higher light intensity 67.6 ± 14.0 mg/dm^2 (n=12).

HPLC and mass spectrometry analysis showed that *I. paraensis* is defended by two major classes of compound: phenolics and saponins. These represented 19.7 ± 3.6% and 7.8 ± 1.5% of leaf mass, respectively. Phenolics were represented by 3-*O*-gallo(epi)catechin (poly)gallate, a compound wide spread in Mimosoideae and present in many *Inga* species (Lokvam, personal observation). While total phenolic compounds increased their mass with light (slope=0.502; R^2=0.172; *p*=0.028; figure 2C), saponins did not vary significantly with light (n=29; slope=0.166; R^2=0.107; *p*=0.083; figure 2D). The combined percentage of phenolic and saponin compounds was positively correlated with light (n=27; slope=0.591; R^2=0.159; *p*=0.039), and increase in total phenolics explained about 21% of the variance in saponins (table 1).

Leaf nitrogen content was positively correlated with saponin content (r_k=0.494; *p*=0.001; table 1), however light had no effect on nitrogen concentration (mean=3.9 ± 0.4%; slope=0.005; R^2=0.002; *p*=0.833; figure 2E). We measured δ^{15}N as an indicator of nitrogen fixation, however, there was no effect of light on δ^{15}N (mean=3.9 ± 0.9‰; slope=0.021; R^2=0.005; *p*=0.715; figure 2F).

We found 30 species of ants visiting the EFNs on *I. paraensis* (table 2). Most ant species (20 in total) were observed at least twice. *Crematogaster* spp. were the most frequent species along the light gradient, representing almost 50% of the observations. *Crematogaster* spp., like the great majority of the species observed (77%), recruit nest mates to a resource. However, *Ectatomma tuberculatum* and *Odontomachus haematodus*, which were also common, are not group foragers. Although there were species that were seen foraging only in shade habitats (e.g. *Solenopsis* sp.A and *Camponotus tenuiscapus*, table 2), dissimilarities in the ant species composition were not related to light environment (r=0.049; *p*=0.173) nor to spatial distance among individual plants (r=-0.020; *p*=0.635). On average, we found 7.8 ± 8.3 ants per plant and 0.9 ± 0.9 ants per EFN. There was no effect of light on number of ants/EFN (slope=-0.001; R^2<0.001; p=0.953; figure 2G).

Individual traits were generally not correlated with light (table 1). A principal components analysis (PCA) grouped plants by combinations of traits. The PCA partitioned the six traits measured into six axes, of which only four individually represented more than 10% of the variance among plants (table 3). These four principal component axes combined to explain 86.7% of the variance among plant traits. The first principal component axis (PC1) distinguished among plants found in shade (< 5% canopy openness) and light (≥ 5% canopy openness) habitats (figure 4), and described leaf chemical traits. Plants that loaded positively on PC1 had a higher concentration of total phenolics, saponins and nitrogen (table 3). Principal components 2-4 highlighted correlations among traits related to leaf production and ant presence (table 3). For instance, leaves from plants that loaded positively on the second principal component axis (PC2) needed more days to expand and they were produced in lower number. On the third principal component axis (PC3), leaves from plants that loaded positively needed fewer days to expand, were also produced in lower numbers and had lower number of ants per EFN. Finally, leaves from plants loading positively on the fourth axis (PC4) needed more days to expand and had lower number of ants per EFN.

Do plant traits affect leaf area consumption?

Rates of herbivory averaged 39 ± 26.5% and ranged from zero percent to total leaf area consumption. 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; figure 2H). Alone, none of the leaf traits was a significant predictor to leaf consumption (figure 5), except for phenolics which showed a weak positive relationship (n=28; slope=3.181; R^2=0.225; p=0.014; figure 5E). However, when we looked at combinations of traits grouped by a PCA, some relationships with herbivory emerged.

Regression models using the first four principal components axes showed that leaf area consumption was significantly correlated with PC2 (table 4). The model predicts that plants having leaves that expanded more slowly (i.e.

those that need more days to fully expand) and that produced fewer leaves would experience lower leaf consumption (n=31; slope=-8.256; R^2=0.098; *p*=0.016). The marginally significant correlation between PC1 and herbivory (n=31; slope=5.113; R^2=0.184; *p*=0.087) shows greater herbivory on leaves with more nitrogen but also more phenolics and saponins.

For model selection based on multiple regressions, leaf consumption was a function of the log-number of leaf per flush and the percentage of total phenolics per leaf (R^2=0.327; *p*=0.004; AIC=82.67; table 5).

Discussion

In general, leaf traits showed remarkably little plasticity in response to light, despite leaf production and phenolics content. We have found responses to the extremes of high light and shade for two traits of *I. paraensis*: a 1.5-fold difference for leaf production and 1.2-fold difference for the mass of phenolics. Our predictions for plasticity among the traits were based in previous studies that have shown large changes in plant traits across light gradients. However, most studies have examined mature leaves (e.g. McKey et al 1978, Nichols-Orians 1991, Folgarait and Davidson 1994, Baraza et al 2004). Our study focused on young, expanding leaves, and in this case, the lack of plasticity suggests strong developmental for phenotypic consistence (i.e. canalization).

Leaf expansion and production

As pointed out initially, young leaves have two main different antiherbivore strategies: ‘defense’ and ‘escape’. Along the defense-escale continuum, *I. paraensis* has relatively fast expanding leaves relative to co-occurring *Inga* species in the study area. They expand three times faster than the slowest species and 1.4 times faster than the median (Coley and Kursar, personal observation). Although we have not measured synchrony, we also suspect that leaf production within local populations of *I. paraensis* tends to be highly synchronous. This trait is predicted to satiate herbivores (Aide 1993). *I. paraensis* also has delayed chloroplast development, a trait that may be a consequence of the fast expansion rate (Kursar and Coley 1992). These characteristics along with our measure of a high herbivory rate suggest that *I. paraensis* can be classified as a species with the escape strategy.

Expansion rate seems to be consistent along the light gradient and the observed variation is more likely to vary due to genetic factors (Grime 1977) rather than environmental conditions. However, leaves produced per flush varied with the light gradient. Grime (1977) argues that leaf production plasticity is a characteristic of better competitors. With respect to our study, we predicted that plants growing in light gap habitats would take advantage of increased resource availability by producing more leaves per flush. Since data for other species in the same forest are not available, we cannot determine whether *I. paraensis* is relatively more or less plastic than other species in the same habitat.

The second principal component axis, PC2, grouped plants according to the escape traits leaf production and leaf expansion. This was the only axis that significantly (positively) correlated with herbivory. Plants loaded positively on PC2 if they produced fewer leaves per flush (or per sapling). The PCA suggests that leaf consumption is reduced in plants with fewer young leaves per flush. While plants may respond with greater growth where there is increased resource availability, herbivores also may be attracted by the increase in young-leaf resources. In Panama, Richards and Coley (2007) found that the higher abundance for herbivore species in gaps was correlated with greater food availability in gaps (i.e. more young leaves). Although we did not find a clear relation between leaf consumption and light habitats, the results from PC2 show that herbivore damage may increase with greater leaf production per sapling.

Plants also loaded positively on PC2 if they expanded their leaves more slowly, thereby lengthening the window of vulnerability to herbivores. Hence, unexpectedly, slower expansion correlated with less damage due to herbivores. In interspecific comparisons, expansion rates are positively correlated with herbivory, but this is because rapid expansion is correlated with other traits that positively affect consumption, such as less effective chemical defenses (Kursar and Coley 2003) and higher nitrogen contents (Kursar and Coley 1991). We did not see any evidence of trade-offs with leaf expansion that could explain the greater damage to slow-expanding leaves (table 1). For two other species of *Inga*, *I. goldmanii* and *I. umbellifera*, Brenes-Arguedas et al (2006) have shown that expansion constrained secondary metabolite production. While slower-expanding species allocated more to phenolic defense production during development, the faster-expanding species produced chemical compounds only early during expansion. Their result matches the predictions of the Growth-Differentiation Balance Hypothesis (Herms and Mattson 1992), which posits that investment in growth and differentiation trades off with investment in defenses. However, Riipi et al (2002) did not find this pattern for Mountain birch leaves. They found that, when leaves declined in growth capacity, phenolic compounds did not accumulate more actively. Instead, phenolics increased throughout the whole leaf growth phase. Our results showed phenolics increasing with greater leaf production per flush (table 1), a measure of plant growth. In our result, the same way as in Riipi et al (2002), growth did not constrain defense investments, contradicting expectations based on the Growth-Differentiation Balance Hypothesis (Herms and Mattson 1992). Our data showed a trend such that, as light increases, *I. paraensis* may invest more in both growth and phenolics defenses.

Leaf chemistry

Among the defensive traits, phenolics were the only one affected by light intensity, highlighting again the little correlation between plasticity in the traits of expanding leaves and the light environments. Both phenolics and saponins are carbon-based compounds. Their concentrations would be expected to increase due to light availability according to the Carbon-Nutrient Balance Hypothesis (Bryant et al 1983). This hypothesis postulates that carbon-based secondary metabolites are determined by the balance between carbon and nutrient availability. Thus, concentrations of such metabolites are expected to increase when carbohydrates are in excess, as a consequence of enhanced photosynthesis. The results of other studies are consistent with the predictions of Carbon-Nutrient Balance Hypothesis for phenolics (Koricheva et al 1998) even when genetic variation was controlled (Mole et al 1988, Henriksson et al 2003). Our phenolic data also support these predictions; however, we did not find evidence to support the main assumption of CNB hypothesis that in high light habitats photosynthesis is enhanced more than growth. Hamilton et al

(2001) had argued that this assumption leads to a mistaken interpretation of growth as the only alternative to defense. We found that individuals in high light habitats increased both growth (leaf production) and investment in defenses (phenolic compounds). This is consistent with the results of a controlled experiment for *Quercus pyrenaica* plant species with water and light variables manipulated (Baraza et al 2004). These observations give little support for the proposed trade-off between growth and defense in Growth-Differentiation Balance and Carbon-Nutrient Balance theories, and suggest that these hypotheses may not explain the physiological mechanisms regulating secondary metabolite production in expanding leaves of *I. paraensis*.

To our knowledge, our study is the first one looking at saponin concentration over a natural light gradient. Despite our expectations based on the Carbon-Nutrient Balance Hypothesis, saponins did not follow the same pattern as phenolics. Differences in allocation to their production could be explained by differences in their biosynthetic pathway and metabolic demands. While phenolics are produced via shikimic acid pathway, saponins are triterpene derivates and, as such, are synthesized from the mevalonic acid pathway (Papadopoulou et al 1999). Because of the different pathways, these compounds would not directly compete for biosynthetic precursors (Haukioja et al 1998). Nevertheless, indirect competition such as for the products of photosynthesis, probably is one possibility. The positive correlation between phenolics and saponins (table 1) suggests a lack of competition between these two groups of metabolites. Thus, metabolic costs for synthesizing compounds may be the main factor differentiating increases in phenolics and saponins (Gershenzon 1994).

Nitrogen content was also not related to increased light, contradicting our expectation of increases due to greater investment in photosynthetic proteins. Another possible explanation for the small response to light could be that, in high light, extra carbon resources were allocated to nitrogen fixation. However, we did not find enough variance in our $\delta^{15}N‰$ values when compared to reference non-fixer plants (Gehring and Vlek 2004) to have confidence in this assertion.

The first PCA axis, PC1, separated plants according to their chemical traits, with greater content of secondary metabolites and nitrogen correlated positively with PC1. The fact that PC1 was positively associated with herbivory, although marginally significantly, suggests that herbivores prefer high nitrogen leaves and are not deterred by the higher secondary metabolite concentrations. Additionally, phenolics were positively correlated with leaf consumption (figure 5E). This unexpected positive correlation of secondary metabolites with herbivory may have two possible explanations.

Investigating within species variation in phenolics, Nichols-Orians (1991) also found positive correlations with leaf consumption. He argued that increases on herbivore damage was specially correlated to secondary metabolites and leaf nitrogen content, such that deterrent effects would be masked by higher nutritional value. Other authors (Sipura and Tahvanainen 2000, Henriksson et al 2003) also reached the same conclusion. Henriksson et al (2003) emphasized that to understand herbivore consumption, nutritive compounds, like water, proteins and sugars, need to be measure additionally to secondary compounds. Although secondary metabolites clearly can have negative effects on herbivores, and species with greater investments generally suffer less damage (for phenolics see: McKey et al 1978, Henriksson et al 2003; for saponins see: Potter and Kimmerer 1989), it may be possible that specialists adapted to feed on a given plant species have the ability to consume those compounds and would therefore be more influenced by nitrogen content.

Another explanation for the evidence that phenolics may not be effective defense takes into account the correlation with gap habitats. Close and McArthur (2002) suggested that the positive relationship between light and phenolics is related to protection from photodamage. They suggest that the greater potential for photodamage in gap habitats, rather than resource availability, is the cause for increases on phenolics production. Moreover other authors (Riipi et al 2002) have also questioned the primary defensive role of phenolics. Riipi et al (2002) found phenolics production to be temporally uniform through leaf development, which led them to conclude that phenolics concentration is not a passive response to resource availability; moreover, phenolics might have several functions only one of which is defense against herbivores.

Ants

The ant assemblage was also not affected by the light gradient, following previous studies carried out in other tropical forests (Feener and Schupp 1998). Feener and Schupp (1998) found no differences between ant abundance or richness between gap and closed understory. Our predictions of higher ant abundance in light habitats were based in studies which showed more nectar production induced by light (Folgarait and Davidson 1994, Bixenmann et al in prep). In our study, we did not measure nectar production to verify our assumptions. If following the overall pattern, there also is a lack of plasticity in this trait in response to light, this could provide a plausible explanation for the fact that ant abundance did not increase with light availability.

Although other authors have attributed better protection to the mutualistic role of ants in *Inga* plants (Koptur 1984, Kersch and Fonseca 2005), specifically shown by ant-exclusion experiments, our observations showed little effect of ants on herbivory. Fáveri et al (2008) conducted experiments of ant predation on artificial caterpillars in our study site and they found lower predation when comparing to studies carried out in other tropical forests, which suggests that ants might be playing a less important defensive role in our study site. Brenes-Arguedas et al (2008) suggest that differences in ant assemblage among sites are important factors in plant selection of defensive traits as the effectivity of ant defenses probably vary from one site to another.

In conclusion, despite large differences in light, we have shown very weak effects of light on *I. paraensis* defensive traits and also weak effects of those traits on leaf consumption. These results suggest that young leaves of *I. paraensis* may have consistent phenotypes. The lack of evidence of different herbivore pressure over *I. paraensis* among the gradient could be an important factor influencing consistence. Alone, traits with potential defensive role showed patterns opposite to the expectations. Experimentally, detriment effects of secondary metabolites are more easily proved. But in field, interaction of plant features may provide more than a nutrition defense dichotomy with unexpected effects on herbivore consumption.

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Fig 1 Predicted light effects on *Inga paraensis* young leaf traits and its effect over leaf area consumption. Solid lines represent the direct effects and broken lines indicate indirect effects. Arrow heads represent positive effects and the filled circles represent negative effects.

Fig 2 Effects of canopy openness on *Inga paraensis* young leaf traits: A) number of leaves per flush (n=92; slope=0.264; z=3.632; $p<0.001$); B) number of days to full leaf expansion (n=42; slope=-0.181; $R^2=0.029$; $p=0.281$); C) percentage of total phenolics in leaf mass (n=28; slope=0.502; $R^2=0.172$; $p=0.028$); D) percentage of saponins in leaf mass (n=29; slope=0.166; $R^2=0.107$; $p=0.083$); E) percentage of nitrogen in leaf mass (n=31; slope=0.005; $R^2=0.002$; $p=0.833$); F) $\delta^{15}N$ per mille (n=31; slope=0.021; $R^2=0.005$; $p=0.715$); G) number of ants per EFN (n=73; slope=-0.001; $R^2<0.001$; $p=0.953$); and H) percentage of leaf area consumption(n=93; slope=0.919; $R^2=0.011$; $p=0.319$).

Fig 3 Chlorophyll content in young leaves of *Inga paraensis* in light and shade habitats ($t=0.341$; $p=0.736$). Boxes are bounded by the first quartile, median, and third quartile; whiskers are 1.5 times the interquartile range.

Table 1 Correlation between pairs of variables associated to *Inga paraensis* young leaves. Upper diagonal values show Kendal tau correlation estimates and lower diagonal values show corresponding *p*-values.

Table 2 Percentage of total ant species observed foraging at *Inga paraensis* extrafloral nectaries (200 observations of 2,205 ants in 109 flushes) in all habitats. Shade habitats= < 5% canopy openness; light habitats= ≥ 5% canopy openness; *= species without recruitment behavior.

Table 3 Principal component analysis results for seven plant traits variables measured over 31 *Inga paraensis* plants. Bold type indicates significant factor loadings (>|0.400|).

Fig 4 Distribution of *Inga paraensis* defined by the first two principal component analysis axes (for PC1 and PC2 details see table 3) based on six young leaf traits. Points are coded as S=shade habitat plants (< 5% canopy openness), L=Light habitat plants (≥ 5% canopy openness).

Fig 5 Effects of *Inga paraensis* young leaf traits on leaf area consumption. A) number of leaves per flush (n=92; slope=0.988; R^2=0.010; *p*=0.346); B) number of days to leaf full expansion (n=42; slope=-0.347; R^2=0.003; *p*=0.752); C) number of ants per extrafloral nectary (EFN) (n=73; slope=-2.190; R^2=0.007; *p*=0.494); D) percentage of nitrogen in leaf mass (n=31; slope=2.823; R^2=0.002; *p*=0.830); E) percentage of total phenolics in leaf mass (n=28; slope=3.181; R^2=0.225; *p*=0.014); and F) percentage of saponins in leaf mass (n=29; slope=2.612; R^2=0.026; *p*=0.420).

Table 4 Linear regressions of percentage of leaf area consumption predicted by the principal components axes which explained more than 10% of variance in *Inga paraensis* plant traits. Summary presents slope values, correlation coefficients (R^2) and *p*-values for each regression. Bold type indicates p>0.05.

Table 5 Multiple regression models of percentage of leaf area consumption. Summary presents models ranked by complexity of predictor variables: logLEAVES= logarithm of the number of leaves per flush; DAYSEXP= number of days to leaf full expansion; sqrtANTS= square-root number of ants per extrafloral nectary; PHENOLIC= percentage of total phenolics in leaf mass; SAPONIN= percentage of saponins in leaf mass; and NITROGEN= percentage of nitrogen in leaf mass. Summary shows correlation coefficients (R^2), *p*-values and Akaike Information Criterion (AIC) value of each model. Bold type indicates the best model based in AIC values.

Figure 1

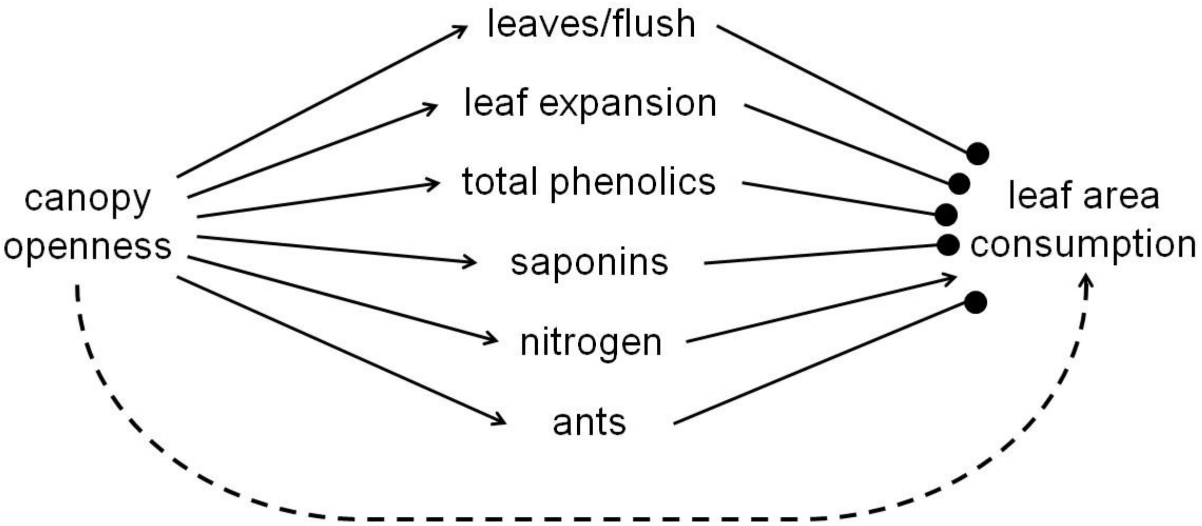

leaves/flush
leaf expansion
total phenolics
canopy openness
saponins
nitrogen
ants
leaf area consumption

Figure 2

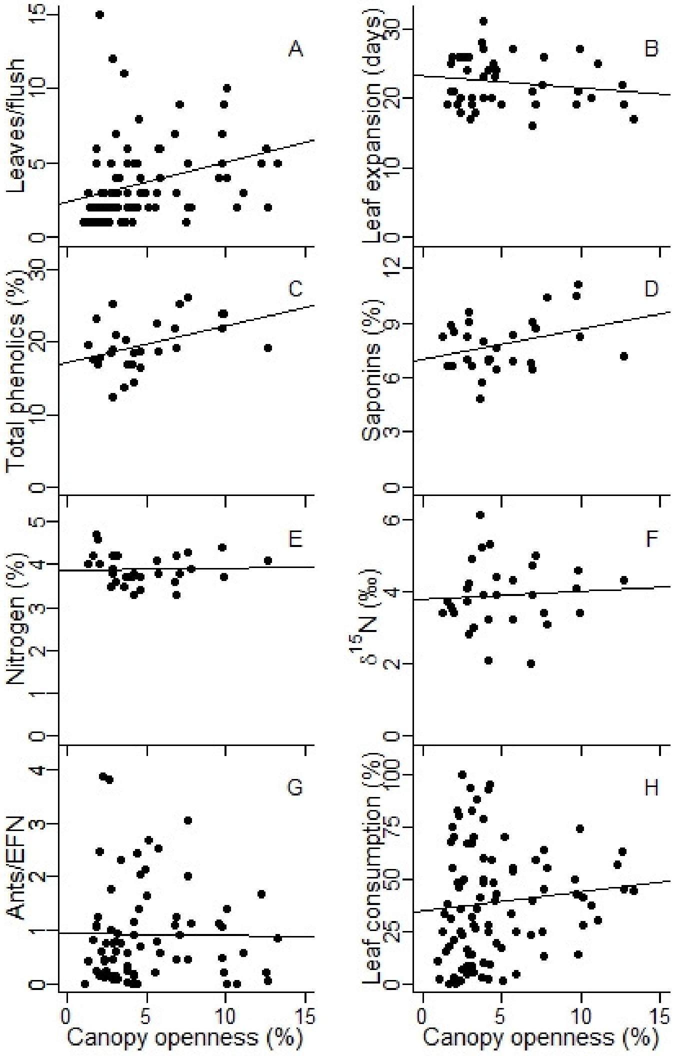

Leaves/flush
0
5
10
15
A
Leaf expansion (days)
0
10
20
30
B
Total phenolics (%)
0
10
20
30
C
Saponins (%)
0
3
6
9
12
D
Nitrogen (%)
0
1
2
3
4
5
E
δ^{15}N (‰)
0
2
4
6
F
Ants/EFN
0
1
2
3
4
G
Leaf consumption (%)
0
25
50
75
100
H
0
5
10
15
Canopy openness (%)
0
5
10
15
Canopy openness (%)

Figure 3

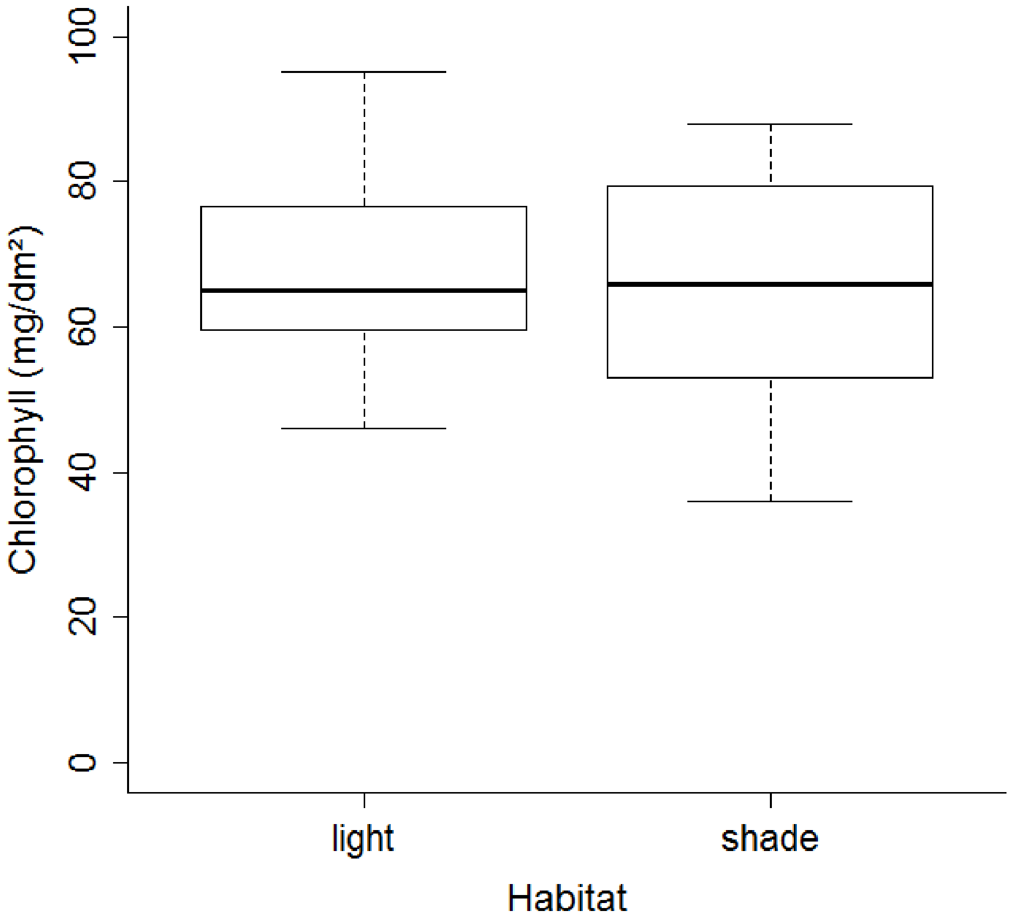


Table 1

p r_k	Canopy openness (%)	Leaves per Flush	Leaf expansion (days)	Ants/EFN	Total phenolics (%)	Saponins (%)	Nitrogen (%)	δ^{15} N (‰)	Leaf area consumption (%)
Canopy openness (%)	---	0.461***	-0.079	-0.317	0.310*	0.127	-0.017	0.271	0.092
Leaves per flush	<0.001***	---	-0.122	-0.124	0.418*	0.135	-0.127	0.451	0.401
Leaf expansion (days)	0.527	0.332	---	-0.009	0.018	0.080	-0.136	-0.332	0.053
Ants/EFN	0.446	0.346	0.845	---	0.142	0.295	0.274	-0.034	0.075
Total phenolics (%)	0.021*	0.036*	0.696	0.797	---	0.458**	0.292	0.230	0.420*
Saponins (%)	0.229	0.799	0.859	0.446	0.004**	---	0.494**	-0.043	0.034
Nitrogen (%)	0.811	0.221	0.947	0.283	0.112	0.001**	---	-0.130	-0.129
δ^{15} N (‰)	0.517	0.073	0.292	0.488	0.634	0.585	0.205	---	0.247
Leaf area consumption (%)	0.170	0.199	0.526	0.569	0.019*	0.225	0.865	0.451	---

Note: Symbols highlight the following significance levels: *p<0.050; **p<0.010; and ***p<0.001.

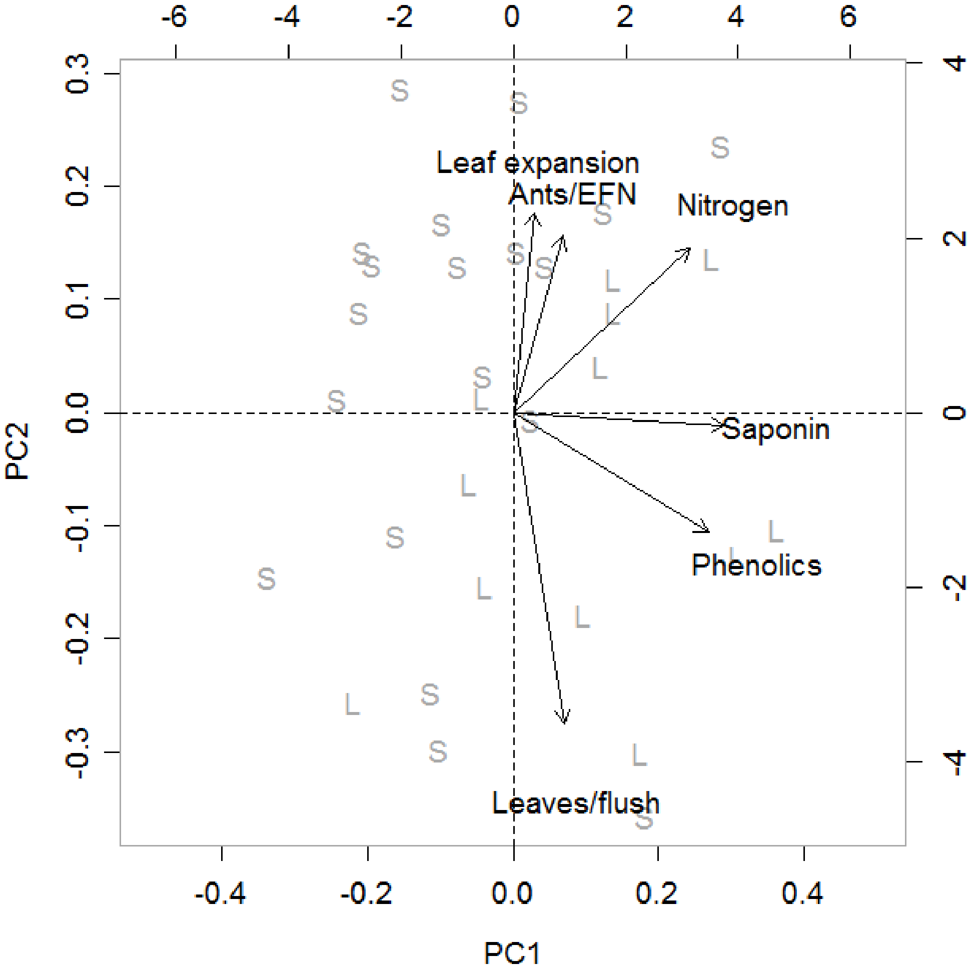
Table 2

	Habitats		
	Both	Shade	Light
Crematogaster spp.	>10	>10	>10
Pheidole sp.13	>10	10	>10
Ectatomma tuberculatum *	6	8	2
Azteca sp.B	5	7	1
Camponotus femoratus	7	6	8
Solenopsis sp.A	3	4	
Camponotus tenuiscapus	2	4	
Pheidole spp.	3	3	2
Solenopsis spp.	1	2	
Cephalotes atratus	1	2	
Brachymyrmex sp.3	1	2	
Brachymyrmex sp.13	1	2	
Azteca sp.A	1	2	
Odontomachus haematodus *	3	<1	5
Azteca spp.	1	<1	1
Wasmannia auropunctata	<1	<1	
Pheidole embolopyx	<1	<1	
Pachycondyla unidentata *	<1	<1	
Odontomachus meinerti *	<1	<1	
Gnamptogenys moelleri	<1	<1	
Dolichoderus bispinosus *	<1	<1	
Crematogaster acuta	<1	<1	
Camponotus crassus	<1	<1	
Paratrechina sp.1	2		4
Ochetomyrmex semipolitus	1		2
Ochetomyrmex sp.	<1		1
Gigantiops destructor *	<1		1
Dolichoderus attelaboides *	<1		1
Cephalotes sp.B	<1		1
Cephalotes sp.A	<1		1

Table 3

Plant traits and PCA parameters	Principal component axes (PCA)			
	1	2	3	4
Log Number of leaves per flush	0.147	**-0.679**	**-0.405**	-0.141
Leaf expansion (days)	0.059	**0.437**	**-0.592**	**0.624**
√ Number of ants per EFN	0.141	0.386	**-0.501**	**-0.740**
% total phenolics in leaf mass	**0.565**	-0.262	-0.265	0.166
% saponins in leaf mass	**0.612**	-0.028	0.248	0.075
% nitrogen in leaf mass	**0.511**	0.360	0.320	-0.102
Eigenvalue	1.910	1.382	1.019	0.889
Cumulative % of variance	0.318	0.549	0.718	0.867

Figure 4



-6
-4
-2
0
2
4
6
0.3
0.2
0.1
0.0
-0.1
-0.2
-0.3
PC2
4
2
0
-2
-4
Leaf expansion
Ants/EFN
Nitrogen
Saponin
Phenolics
Leaves/flush
S
L
-0.4
-0.2
0.0
0.2
0.4
PC1

Fig 5

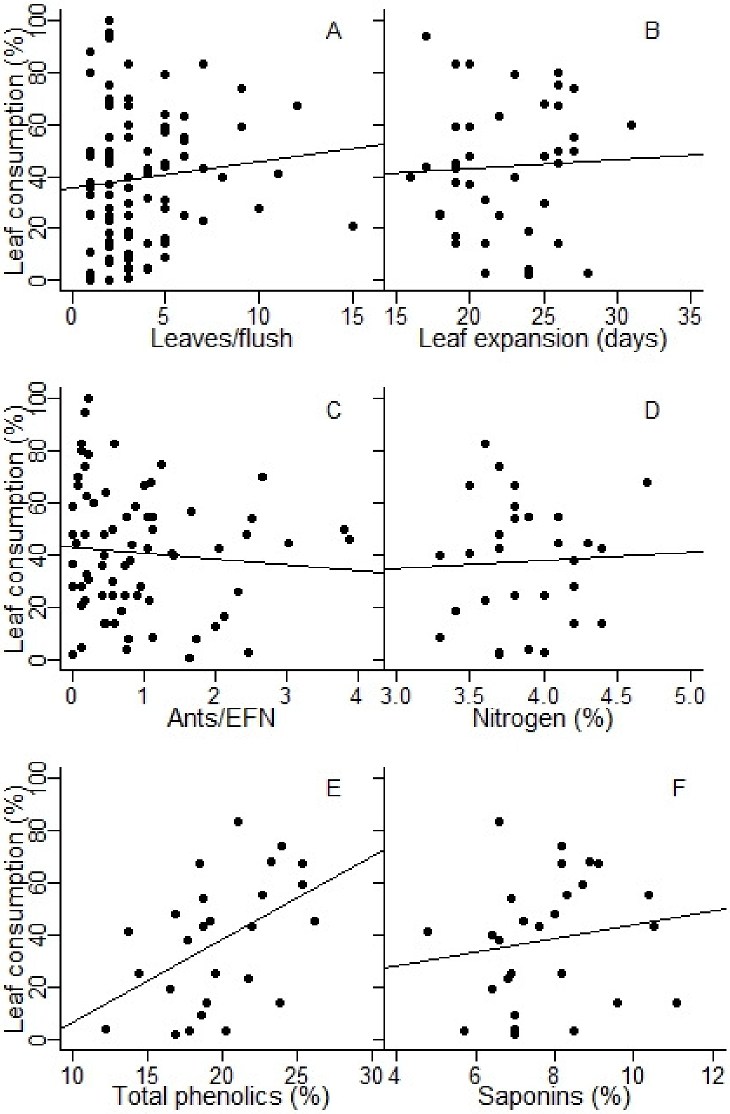

A
B
C
D
E
F
Leaf consumption (%)
0
20
40
60
80
100
Leaves/flush
0
5
10
15
Leaf expansion (days)
15
20
25
30
35
Ants/EFN
0
1
2
3
4
Nitrogen (%)
3.0
3.5
4.0
4.5
5.0
Total phenolics (%)
10
15
20
25
30
Saponins (%)
4
6
8
10
12

Table 4

Predictor variable	slope	R^2	*p*
PC1	5.113	0.098	0.087
PC2	**-8.256**	**0.184**	**0.016**
PC3	-3.833	0.029	0.358
PC4	0.848	0.001	0.850

Table 5

Predictor variables	R^2	*p*	AIC
logLEAVES* + DAYSEXP + sqrtANTS + PHENOLIC* + SAPONIN + NITROGEN	0.343	0.092	89.93
logLEAVES* + sqrtANTS + PHENOLIC* + SAPONIN + NITROGEN	0.341	0.051	88.02
logLEAVES* + sqrtANTS + PHENOLIC* + SAPONIN	0.337	0.026	86.22
logLEAVES** + sqrtANTS + PHENOLIC*	0.335	0.011	84.33
logLEAVES + PHENOLIC***	**0.327**	**0.004**	**82.67**
logLEAVES***	0.231	0.006	84.81

Note: Symbols highlight the following significance levels for the predictor variables: *p<0.100, **p<0.050 and ***p<0.010.

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CONCLUSÕES

1) Apesar de grandes diferenças na incidência luminosa, nós mostramos um efeito fraco da intensidade luminosa sobre as características de defesa de *Inga paraensis* na Amazônia Central e também um efeito fraco dessas características no consumo foliar por herbívoros.

2) Os resultados sugerem que folhas jovens de *I. paraensis* apresentam desenvolvimento canalizado possivelmente relacionado a fisiologia. A falta de evidência de uma pressão por herbívoros sobre *I. paraensis* ao longo do gradiente de luz pode ser um importante fator influenciando essa canalização no desenvolvimento.

3) Outro importante padrão encontrado é que as defesas contra herbívoros parecem ser promovidas pela combinação de diferentes características. Individualmente, as características possuem fraco papel defensivo, e especificamente para fenóis, não muito bem compreendido. Experimentalmente, os efeitos repelentes dos metabólitos secundários são mais facilmente corroborados. Todavia, no campo, a sinergia entre as diferentes características das plantas não se limitam ao dualismo entre nutrição e defensa gerando assim efeitos não esperados sobre o consumo por herbívoros.

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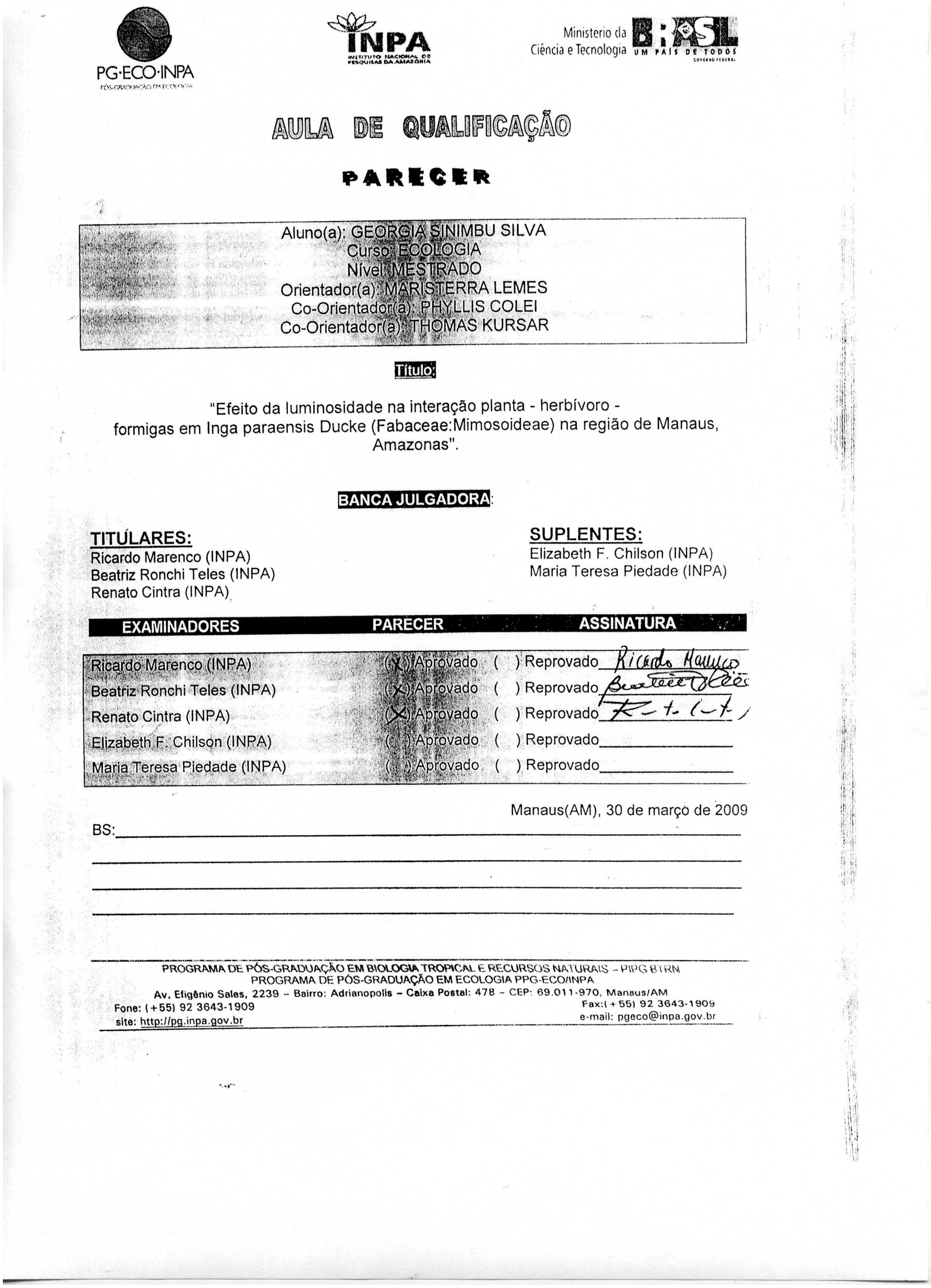
ANEXO A – Ata da aula de qualificação



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AULA DE QUALIFICAÇÃO

PARECER

Aluno(a): GEORGIA SINIMBU SILVA
Curso: ECOLOGIA
Nível: MESTRADO
Orientador(a): MARISTERRA LEMES
Co-Orientador(a): PHYLLIS COLEI
Co-Orientador(a): THOMAS KURSAR

Título:

"Efeito da luminosidade na interação planta - herbívoro - formigas em Inga paraensis Ducke (Fabaceae:Mimosoideae) na região de Manaus, Amazonas".

BANCA JULGADORA:

TITULARES:
Ricardo Marenco (INPA)
Beatriz Ronchi Teles (INPA)
Renato Cintra (INPA)

SUPLENTES:
Elizabeth F. Chilson (INPA)
Maria Teresa Piedade (INPA)

EXAMINADORES	PARECER	ASSINATURA
Ricardo Marenco (INPA)	(X) Aprovado ( ) Reprovado	Ricardo Marenco
Beatriz Ronchi Teles (INPA)	(X) Aprovado ( ) Reprovado	
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Maria Teresa Piedade (INPA)	( ) Aprovado ( ) Reprovado	

Manaus(AM), 30 de março de 2009

BS:

PROGRAMA DE PÓS-GRADUAÇÃO EM BIOLOGIA TROPICAL E RECURSOS NATURAIS – PIPG BTRN
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ANEXO B – Ata da defesa oral

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ATA DA DEFESA PÚBLICA DA DISSERTAÇÃO DE MESTRADO DO PROGRAMA DE PÓS-GRADUAÇÃO EM ECOLOGIA DO INSTITUTO NACIONAL DE PESQUISAS DA AMAZÔNIA.

Aos 29 dias do mês de julho do ano de 2010, às 14:30 horas, na sala de aula do Programa de Pós-Graduação em Ecologia PPG-ECO/INPA, reuniu-se a Comissão Examinadora de Defesa Pública, composta pelos seguintes membros: **Dra. Flávia Regina Capellotto Costa**, do Instituto Nacional de Pesquisas da Amazônia, **Dr. José Luis Campana Camargo**, do Projeto Dinâmica Biológica de Fragmentos Florestais PDBFF/INPA, **Dr. Ricardo Antônio Marenco**, do Instituto Nacional de Pesquisas da Amazônia, tendo como suplentes o Dr. Renato Cintra Soares, do Instituto Nacional de Pesquisas da Amazônia, e o Dr. José Francisco Carvalho, do Instituto Nacional de Pesquisas da Amazônia, sob a presidência do(a) primeiro(a), a fim de proceder a argüição pública da **DISSERTAÇÃO DE MESTRADO** de **GEORGIA SINIMBU SILVA**, intitulada "Efeito da luminosidade nas características de defesa contra herbívoros de *Inga paraensis* Ducke (Fabaceae: Mimosoideae)", orientada pela Dra. Maristerra Rodrigues Lemes, do Instituto Nacional de Pesquisas da Amazônia e co-orientada pelos Drs. Phyllis D. Coley e Thomas A. Kursar, ambos da Universidade de UTAH (USA).

Após a exposição, o(a) discente foi argüido(a) oralmente pelos membros da Comissão Examinadora, tendo recebido o conceito final:

☒ APROVADO(A) ☐ REPROVADO(A)

☒ POR UNANIMIDADE ☐ POR MAIORIA

Nada mais havendo, foi lavrada a presente ata, que, após lida e aprovada, foi assinada pelos membros da Comissão Examinadora.

Dr(a). Flávia Regina Capellotto Costa ____________________

Dr(a). José Luis Campana Camargo José L. ____________________

Dr(a). Ricardo Antônio Marenco Ricardo Marenco ____________________

Claudia Keller
Coordenação do PPG-ECO/INPA

Beatriz Ronchi Teles
Coordenação de Capacitação do INPA