Plant Ecol (2014) 215:209–220
DOI 10.1007/s11258-013-0290-y

Leaf synchrony and insect herbivory among tropical tree habitat specialists

Greg P. A. Lamarre · Irene Mendoza ·
Paul V. A. Fine · Christopher Baraloto

Received: 23 April 2013 / Accepted: 13 December 2013 / Published online: 11 January 2014

Abstract Growth defense tradeoff theory predicts that plants in low-resource habitats invest more energy in defense mechanisms against natural enemies than growth, whereas plants in high-resource habitats can afford higher leaf loss rates. A less-studied defense against herbivores involves the synchrony of leaf production, which can be an effective defense strategy if leaf biomass production exceeds the capacity of consumption by insects. The aim of this study was to determine whether leaf synchrony varied across habitats with different available resources and whether insects were able to track young leaf production among tree habitat specialists in a tropical forest of French Guiana. We predicted that high-resource habitats would exhibit more synchrony in leaf production due to the low cost and investment to replace leaf tissue. We also expected closer patterns of leaf synchrony and herbivory within related species, assuming that they shared herbivores. We simultaneously monitored leaf production and herbivory rates of five pairs of tree species, each composed of a specialist of *terra firme* or white-sand forests within the same lineage. Our prediction was not supported by the strong interaction of habitat and lineage for leaf synchrony within individuals of the same species; although habitat specialists differed in leaf synchrony within four of five lineages, the direction of the effect was variable. All species showed short time lags for the correlation between leaf production and herbivory, suggesting that insects are tightly tracking leaf production, especially for the most synchronous species. Leaf synchrony may provide an important escape defense against herbivores, and its expression appears to be constrained by both evolutionary history and environmental factors.

Communicated by William E. Rogers.

G. P. A. Lamarre (✉)
Université Antilles Guyane, UMR Ecologie des Forêts de Guyane, 97310 Kourou, French Guiana
e-mail: greglamarre973@gmail.com

G. P. A. Lamarre · C. Baraloto
INRA, UMR Ecologie des Forêts de Guyane,
97310 Kourou, French Guiana

I. Mendoza
Plant Phenology and Seed Dispersal Research Group,
Departamento de Botânica, Instituto de Biociencias,
Universidade Estadual Paulista (UNESP), Avenida 24-A
no 1515, Rio Claro CEP 13506-900, Brazil

I. Mendoza
UMR 7179 CNRS-MNHN, Departement d'Ecologie et
Gestion de la Biodiversité, Muséum National d'Histoire
Naturelle, 1 Av. du Petit Château, 91800 Brunoy, France

P. V. A. Fine
Department of Integrative Biology, University of
California, 1005 Valley Life Sciences
Building Number 3140, Berkeley, CA 94720, USA

C. Baraloto
Department of Biology, University of Florida,
Gainesville, FL 32611, USA

Keywords Phenology · Escape · Herbivorous insects · Resource availability · Time lag · French Guiana

Introduction

Damage to leaves by herbivores can have a significant impact on plant ecological strategies (Coley and Kursar 1996; Marquis 1984). Many plant strategies against insect herbivores have been well-described, including chemical defenses (Becerra 1997; Herms and Mattson 1992; Kursar and Coley 2003), plant structural traits (Hanley et al. 2007), and indirect defenses, such as production of extrafloral nectar and emission of volatiles that can attract enemies of herbivores (Bixenmann et al. 2013; Heil and Kost 2006). Although some young leaves are chemically defended, their high concentration of water and nitrogen in addition to low leaf toughness renders them highly vulnerable to natural enemies during this stage (Coley and Kursar 1996; Herms and Mattson 1992). A less-studied defense strategy involves the synchrony of leaf production—i.e., a simultaneous leaf emergence at the plant population level such that leaf biomass of a population of conspecifics exceeds the capacity of consumption by insects (Aide 1993).

Several classic studies have shown that rapid and synchronous flushes of leaf production may contribute to plant escape from their natural enemies (Feeny 1976; McKey 1975). Plant escape takes place during leaf expansion when herbivores are at low density (e.g., seasonal escape, see Aide 1992) and subsequently the leaves became mature and unpalatable before an increase in herbivore populations can access the vulnerable leaf tissue (Lieberman and Lieberman 1984). In tropical forests, synchronous leaf production of young leaves has been shown to reduce leaf damage by satiating leaf-feeders (Aide 1988, 1993; McKey 1975). Insect satiation is the most plausible explanation for this phenomenon and it implies that specialist leaf-feeding insects are limited in their population sizes and not being capable of consuming the majority of expanding leaves before they mature. If insect populations are responding to newly produced leaves, then there should be a short time lag between peaks of leaf production and herbivory. In contrast, a more continuous leaf production (e.g., asynchrony) within the community of conspecifics is less likely to reduce overall damage via escape because a constant insect population would consume a higher proportion of the available new leaf tissue. However, insect populations might not be limited by leaf production, and asynchronous leaf production might therefore translate in a loose tracking by insects. This situation would favor more direct plant defense mechanisms such as leaf toughness, secondary metabolites, toxic compounds, and/or extrafloral nectaries (Bixenmann et al. 2013; Coley and Kursar 1996; Macauley and Fox 1980; McKey 1989). Although synchrony has been effectively linked to herbivory reduction in tropical forests (Aide 1988, 1993; Coley and Kursar 1996), no one has investigated how leaf synchrony may change across a resource gradient in tropical forests.

Resource allocation theory predicts that plants growing in low-resource habitats would invest more in defense mechanisms against herbivores at the expense of growth, because of the high cost of tissue replacement (Coley et al. 1985; Fine et al. 2006). In contrast, plant species growing in high-resource habitats are predicted to allocate more resources to leaf and stem production because of the lower cost of leaf replacement. In addition, the larger presence of the third trophic level in resource-rich habitats might allow plants to persist with a lower defense investment (Mooney et al. 2010). Leaf synchrony is another defense mechanism that would allow plants to avoid insect herbivores, and could represent an alternative to constitutive defense strategies like secondary metabolites. On one hand, it would be expected that synchronous leaf production would be more common in high-resource habitats, because of the lower cost of leaf production (Coley et al. 1985) and the higher abundances of herbivores (Mooney et al. 2010; Fine et al. 2013). The lower cost of leaf production in high-resource habitats means that for each plant, they could produce more leaves per capita per year, and thus synchrony may be more likely. However, low-resource habitats could also select for synchrony in plants if the cost of producing new leaves were lower during certain time periods because of temporal variation in resource availability. It is therefore necessary to understand whether leaf production synchrony, as a phenological antiherbivore defense, is linked to resource availability of a habitat in order to fully understand the defense mechanisms of plants against natural enemies.

Contrasting environmental conditions may select for different ecological strategies in tropical trees including defense strategies against herbivores (Fine et al. 2004, 2006). Recently, Fortunel et al. (2014) showed that plant species growing in low-resource habitats such as white-sand forests had denser and thicker leaves than species growing in high-resource habitat (e.g., *terra firme* clay forest). In low-resource habitats, environmental filtering can indeed favor species with resource conservation strategies (i.e., long leaf life span) as has been found in white-sand forest tree specialists. In a previous study, long-term monitoring did not find strong support for the growth defense tradeoff theory for contrasted habitats including white-sand and *terra firme* clay forests, as there was not a general positive relationship between indices of herbivory and leaf production rates (Lamarre et al. 2012). This study showed that some fast-growing species experienced low herbivory rates without large investment in defense strategy (e.g., *Protium* species); a pattern that the authors suggested was consistent with a cost-effective herbivore escape strategy through time and/or space.

Here, we simultaneously examined patterns of the synchrony of leaf production and insect herbivory within two common tropical forest habitats in lowland Amazonia that contrast markedly in soil resource availability (Baraloto et al. 2011): (1) *terra firme* clay forests with high nutrient availability (hereafter, TF), and (2), white-sand forests with low nutrient availability that are often distributed in forest patches (hereafter WS). As outlined above, we predicted that synchrony of leaf production would be more common in high-resource environments (TF) than in low-resource environments (WS) because the cost and the investment of leaf production are thought to be lower in TF than in WS (Coley et al. 1985; Coley and Kursar 1996). In addition, we expected that synchronous leaf flushing among conspecifics would assist plants in avoiding damage from herbivore insects. We therefore predicted that the time taken by insects to damage recently produced leaves—i.e., time lags between leaf production and herbivory damage—can shed light on how plants may escape herbivore damage, with shorter time lags indicating a closer tracking of insects to leaf production.

Closely related plant species are more likely to share common natural enemies (Ehrlich and Raven 1964) in addition to defense strategies (Agrawal et al. 2009). We therefore controlled for phylogeny by studying five monophyletic tree lineages that employ diverse types and different amounts of physical and chemical defense strategies (Lamarre et al. 2012), with one focal species of each lineage specialized to each habitat type. We predicted that within-lineage leaf synchrony would be stronger than among-lineage leaf synchrony. This study addresses the following questions: (1) how does the synchrony of leaf production vary among lineages and habitats? (2) To what extent are natural enemies tracking leaf production and its variation among lineages and habitats?

Materials and methods

Study sites and focal tree species

Our study plots were located at the Laussat Conservation Area in French Guiana (05°28′N, 053°35′W). Climate in the region is driven by a seasonal alternation between wet (December to February and April to July) and dry seasons (September to November and March). According to phenological information using remote sensing or LIDAR methods, a peak of leaf production in French Guiana mostly occurs at the beginning of the dry season when solar radiation is maximal (Pennec et al. 2010; Wagner et al. 2013). In our study, field surveys lasted from March to July 2012, corresponding in French Guiana to one complete rainy season and a short dry season in March (Bonal et al. 2008).

We studied five lineages: *Inga* (Fabaceae), *Protium* (Burseraceae), Bombacoideae (Malvaceae), *Micropholis* (Sapotaceae), and *Licania* (Chrysobalanaceae). We selected these lineages because they are phylogenetically dispersed within the eudicots, the dominant angiosperms in tropical rain forests, and are widespread in the Amazon basin and the Guiana Shield. From each lineage, we chose one species that was common in each habitat type and infrequent or absent in the other (Lamarre et al. 2012). Plant monitoring was conducted in a 2-ha area in each habitat type and were seperated by 1 km. The spatial configuration followed a modified Gentry plot, composed of ten staggered lines (100 m) perpendicular to a central line (180 m; see Baraloto et al. 2011, 2013). We measured leaf production and herbivory rates in 8–20 individuals per species according to their abundance in each plot.

Insect herbivory and leaf production rates

We monitored conspecific saplings separated by at least 10 m to avoid spatial autocorrelation due to related attacks on adjacent plants. Leaf phenology and herbivory measurements were performed on saplings from 1 to 4 m height because understory saplings receive higher proportion of herbivory attacks (Coley and Kursar 1996). We controlled for light availability with all individuals sharing a crown exposure index of 2 or less; that is, no individual received direct overhead or lateral sunlight (see Poorter et al. 2006). We monitored a total of 172 juvenile trees weekly during a 4-month period (17 censuses). During each census, we tagged new leaves produced since the week before using colored wire and we counted the number of produced, damaged and defoliated leaves. We estimated the proportion of the leaf area removed each week using transparent sheets with a 5 mm grid. We calculated an index of Leaf Production Rate (hereafter LPR) for each individual and census, as follows:

$$\text{LPR } tn = \frac{\text{leaf blades produced at } tn}{\text{Initial leaf blades count} + \sum_{i=1}^{N} \text{weekly blades produced}},$$

where tn is the census at week n and N is the total number of weeks during which we carried out our study. Because most herbivore damage occurs during the first weeks of leaf expansion (Coley 1980), leaf expansion time was monitored in our study for each week (see Lamarre et al. 2012). We estimated an herbivory rate (hereafter HR) for each individual and census using a linear approximation of the surface area removed during leaf expansion, averaged for all observed leaves to a composite measure for each individual as:

$$\text{HR } tn = \frac{\sum_{i=1}^{n} \text{No. of damaged blades at } tn \times \overline{\text{Herbivory}} \text{ at } tn}{\sum_{i=1}^{N} \text{weekly blades produced}} \Bigg/ 100,$$

where $\overline{\text{Herbivory}}$ is the mean of the accumulated surface removed by herbivores of all the leaves showing damage at time tn. HR includes defoliated leaves due to herbivore or pathogen attack (assigning a value of 100 % as Aide 1993). During the period of our study, the most abundant groups of herbivores observed were Chrysomelidae, Curculionidae (Coleoptera), and Cicadellidae (Hemiptera).

Data analyses

To estimate synchrony in leaf production (Question 1), we calculated two proxies. First, we calculated the variance of the peaks of leaf production at the population level. Each peak (hereafter *Tmax*) was calculated as the week at which leaf production rate was greatest for each individual, and indicates the timing or seasonality of leaf production at an individual level. We measured synchrony as the variance in these *Tmax* values among all individuals in each population. The second proxy of leaf synchrony (hereafter *week90*), indicated the number of weeks necessary to encompass the 90 % of individuals of a given species having reached their peak of leaf production (following Augspurger 1983). For calculating this index we estimated first the percentage of individuals that reached their *Tmax* at each census, and then counted the number of weeks that included the 90 % of them. We estimated leaf investment as the total number of produced leaves per individual at the end of the study, and we estimated overall herbivory impact as the total number of damaged leaves. We tested differences among habitats and lineages in our four response variables (*Tmax*, *week90*, number of produced leaves, and number damaged leaves) using a Generalized Linear Model with a Poisson distribution (Bolker et al. 2009).

To estimate the temporal correlation among the timing of leaf production and herbivory rate (Question 2), we used a cross-correlation analysis between the weekly values of LPR (used as the explanatory variable) and the differences in HR among censuses (used as the response variable) for each individual that had produced at least one new leaf during the monitoring time (Legendre and Legendre 1998). We extracted the week lags that significantly maximized each cross-correlation and explored differences in positive lags among habitats and lineages using a binomial Generalized Model. We used a stepwise variable selection based on the Akaike Information Criterion (AIC) to select the best statistical model in all cases (Burnham and Anderson 1998). Statistical analyses were performed with R software 2.15.1 (R Development Core Team 2012).

Results

Leaf synchrony among lineages and between habitats

The five tree lineages displayed contrasting patterns in their timing of leaf production (Fig. 1; Table 1). Our index of synchrony estimation *Tmax* varied across habitats in different ways across lineages (lower AIC for the saturated model with interactions; Table 2). Four of the ten studied taxa showed a high degree of synchrony, reflected by the low variance of *Tmax* (Fig. 1): the two *Protium* species (Burseraceae), *Micropholis egensis* (Sapotaceae) and to a lesser extent *Eriotheca longitubulosa* (Bombacoideae). Although the variance of *Tmax* did not follow a consistent trend for higher synchrony in *terra firme* than white-sand specialists, we found a significant effect of habitat for the proxy of leaf synchrony *weeks90* (mean values; TF = 10.4 and WS = 15 weeks; in this model the interaction term was not included because we only had one *week90* value per species). Accordingly, both *Protium* species showed 90 % of individuals' peak of leaf production at relatively short time intervals (i.e., 11 weeks; Table 1).

The *Micropholis* species growing in *terra firme* forest (*M. egensis*) showed a very interesting pattern regarding its timing of leaf production, with the peaks of leaf production of the entire population concentrated in only 3 weeks (Fig. 1; Table 1). In contrast, *Micropholis guyanensis* from the low-resource habitat (WS) showed a stable and continuous leaf production without any distinct peaks throughout the entire wet season (Fig. 2). All tree species growing in WS habitat except *Protium aracouchini* showed continuous leaf production during the period of study. We observed that this pattern was not exclusive to the low-resource habitat as tree specialists from TF and WS in *Inga* and *Licania* lineages were continuously producing leaves throughout the 4-month period (Figs. 1, 2).

Despite our prediction of differences in phenological patterns of leaf production between the white-sand and the *terra firme* clay forest communities, the number of produced and damaged leaves also showed a significant interaction term for habitats and lineages (lower AIC for the saturated model; Table 2). Except for Bombacoideae, there were significantly more leaves produced in TF than in WS. In addition, we found a higher number of damaged leaves in the high-resource habitat than in the low-resource habitat (Table 1), as predicted by the resource allocation theory.

Phenology of host plant and natural enemies

We found contrasting responses among species in the correlation between the timing of herbivory and leaf production (Fig. 2; Tables 1, 2). The 75.4 % of individuals showed significant correlations between LPR and HR and from those, the 97.03 % had a positive sign. In addition, all species showed an elevated number of positive lags between LPR and HR—i.e., the peak of maximum herbivory reached after the peak of maximum leaf production—except for *M. guyanensis* (Fig. 3). In particular, the *Protium* lineage showed 85 and 75 % of positive lags in TF and WS habitats, respectively (Fig. 2; Table 1). The percentage of positive lags was also very high for the Bombacoideae. For almost all individuals, the peak arrival of insect herbivores in both *Inga* plant populations occurred the week after the plants were producing the greatest number of leaves (Fig. 2). More than 85 % of the total foliage produced by the study population of *Inga pezizifera* was consumed by insects in less than 4-weeks. In summary, within each lineage the proportion of positive lags was higher for TF (73.6 ± 24.2 %; mean ± SD) than WS specialists (59.4 ± 27.0 %; mean ± SD) and the interaction term of habitat and lineage did not significantly increase the explained variance (Table 2).

Discussion

Our study assessed the synchrony of leaf production and herbivory in tropical rainforest at a fine temporal scale. We simultaneously monitored leaf production and insect herbivory rate from habitat specialists of *terra firme*, the high-resource habitat (TF), and white-sand forests, the low-resource habitat (WS), within five tropical tree lineages. Contrary to our prediction, we found a strong interaction of habitat and lineage for leaf synchrony measured in terms of the variance of

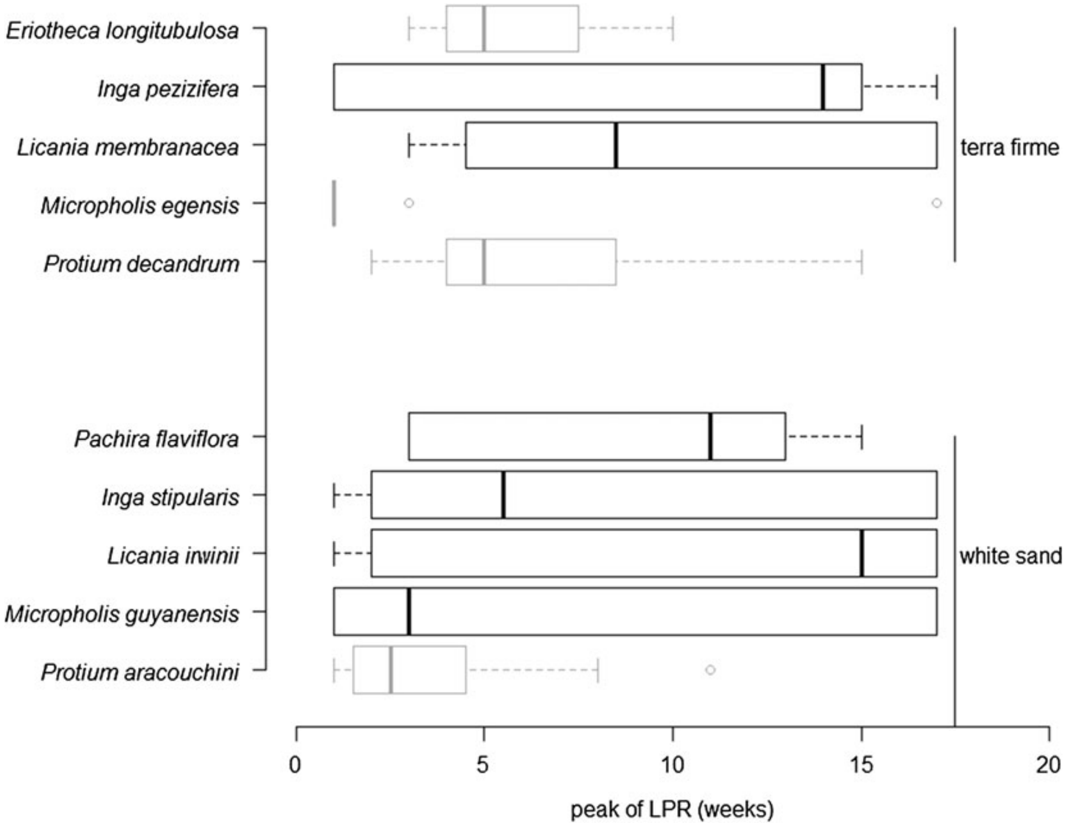

Fig. 1 Boxplots illustrating differences among the ten focal species for the peaks of leaf production rates (*Tmax*). *Grey plots* represent tree species that showed leafing synchrony, and *black plots* those that showed continuous leaf production. The *top panels* represent the *terra firme* specialists and the *bottom panels* represent white-sand tree specialists

Tmax, although the number of weeks necessary for reaching the peaks of leaf production for the 90 % of the individuals (*weeks90*) was significantly shorter in TF than WS. We also emphasize that all tree species showed short time lags for the correlation between leaf production and insect herbivory, especially the most synchronous species, indicating that herbivorous insects are tightly tracking leaf production in tropical forests.

Variation in leaf synchrony among habitat and lineages

Although our expectation was to find higher leaf synchrony in TF than in WS, we only detected an effect of habitat type on leaf synchrony for the variable *week90* (Table 2). By contrast, for all the proxies of leaf production we used and the variance of *Tmax*, we found an interaction among habitat and lineage (Table 2). Those variables showed a strong effect of habitat, but the direction of the effect differed among lineages. Although light conditions, microclimate and soil fertility clearly differ between the two habitats (Baraloto et al. 2011), our models showed the poorest support for habitat alone (Table 2).

Allocation to growth for plant species in low-resource habitats is expected to be lower than in high-resource habitats because of the generally low availability of nutrients (growth defense tradeoff theory, see Coley et al. 1985; Fine et al. 2004). However, we found that tree populations growing in WS were able to simultaneously produce many new leaves, in particular for the studied *Protium* WS specialist. For example, one individual of *P. aracouchini* in WS produced more than 400 leaves in 2 weeks. This pattern suggests that some species growing in a low-resource habitat are able to acquire enough resources (light, water, and nutrients) to produce a large number of new leaves in a short time lag. One reason for this

Table 1 Summary of some descriptive variables of leaf production and herbivory damage

Lineage (family)	Species	Habitat	Individuals without LPR (%)	Average number of produced leaves	Average number of damaged leaves	%Positive lags	Lag weeks (mean ± SD)	*week90*
Bombacoideae (Malvaceae)	*Pachira flaviflora*	WS	25.00	24.67 ± 10.74	16.11 ± 12.60	85.70	2.14 ± 2.73	13
	Eriotheca longitubulosa	TF	70.00	21.67 ± 11.15	11.67 ± 10.26	100.00	0.67 ± 0.58	8
Inga (Fabaceae)	*Inga stipularis*	WS	10.00	25.17 ± 20.90*	13.67 ± 12.85*	68.75	1.55 ± 2.34	17
	Inga pezizifera	TF	23.81	30.50 ± 28.59*	21.69 ± 20.06*	85.71	1.00 ± 1.21	15
Licania (Chrysobalanaceae)	*Licania irwinii*	WS	5.26	23.39 ± 19.71*	10.39 ± 9.70*	47.06	2.25 ± 2.71	17
	Licania membranacea	TF	0	54.55 ± 40.36*	41.75 ± 36.27*	42.11	3.88 ± 2.17	15
Micropholis (Sapotaceae)	*Micropholis guyanensis*	WS	5.56	24.00 ± 11.93*	11.94 ± 9.54*	18.75	6.67 ± 1.53	17
	Micropholis egensis	TF	0	17.36 ± 13.45*	6.86 ± 7.80*	54.55	2.50 ± 0.84	3
Tribe Protieae (Burseraceae)	*Protium aracouchini*	WS	15.79	83.44 ± 111.04*	23.62 ± 21.29*	75.00	3.08 ± 2.47	11
	Protium decandrum	TF	15.79	21.94 ± 15.55*	17.56 ± 14.37*	85.71	1.58 ± 2.47	11

The dependent variable *week90* is the number of weeks necessary for including the 90 % of individuals showing peaks of leaf production. Except for the percentage of individuals without leaf production and *week90*, values represent mean ± SD. Asterisk indicates significant differences of habitat type within lineages according to contrast analyses

pattern could be resource seasonality. In this sense, poor soils and frequent drought stress of white-sand forests might favor species that produce a large number of leaves all at once at the beginning of the wet season, which might represent a lower cost than producing leaves continuously. Additional physiological processes such as the balance between leaf construction cost and photosynthesis with regards to environmental cues (rainfall seasonality, temperature, photoperiod, and solar irradiance) may also influence leaf production and synchrony (Lieberman and Lieberman, 1984; Van Schaik et al. 1993).

During the study period, only the *Protium* lineage showed a consistent pattern of high leaf synchrony in both habitats (Fig. 1). We therefore envision that this lineage may have a stronger conservative phenology than the other studied lineages. Other studies in the Neotropics also showed that antiherbivore defense type could be phylogenetically conserved in some *Burseraceae* lineages (i.e., all *Bursera* species produce monoterpenes, Becerra 1997). It is indeed fascinating that both *Protium* species exhibited strong synchrony patterns in contrasting forest habitats; however, we realize that these are only 2 of the more than 30 *Protium* species occurring in French Guianan rainforests (Molino et al. 2009) and further monitoring of other species is needed before reaching any conclusions about clade-level patterns.

Micropholis was the only lineage that followed our prediction of higher synchrony of leaf production in TF habitats. *Micropholis egensis*, which is strongly associated with *terra firme* habitats, showed the highest degree of leaf synchrony (according to the two proxies of synchrony), whereas *M. guyanensis*, from the white-sand forest, showed a continuous leaf production and received nearly twice as much leaf damage as individuals of the species in *terra firme* habitats (Table 1). We speculate that the synchronous leaf production of *M. egensis* may subsequently affect the level of herbivory and potentially lowers the impact of natural enemies in its habitat of origin (i.e., the high-resource habitat). In contrast, *Licania* and *Inga* lineages produced leaves continuously over at least 15 weeks through the entire wet season (Fig. 2; Table 1). We speculate from our field observations that both lineages may have evolved other defense strategies to reduce the impact of herbivory such as extrafloral nectaries for *Inga* (Pennington et al. 1997; Bixenmann et al. 2013) or delayed greening for

Table 2 Summary of the models used in this work analyzing the influence of habitat and lineage on the peaks of leaf production (*Tmax*), the number of weeks when the 90 % of the individuals showed peaks of leaf production (*week90*), the proportion of positives lags in the cross-correlation between LPR and HR (*positive lags*), the number of newly *produced leaves*, and the number of leaves damaged by insects (*damaged leaves*)

Dependent variable	Predictor variables	AIC	ΔAIC	Residual deviance	Residual df
Tmax	Habitat × lineage	1156.5	**0**	636.16	136
	Lineage	1193.5	37	683.12	141
	Habitat + lineage	1195.3	38.8	682.94	140
	Null	1290.1	133.6	787.74	145
	Habitat	1292.1	135.6	787.71	144
week90	Habitat	60.778	**0**	13.774	8
	Null	62.967	2.189	17.963	9
	Lineage	65.274	4.496	12.27	5
positive lags	Habitat + lineage	162.32	**0**	150.32	128
	Lineage	163.16	**0.83**	153.16	129
	Habitat × lineage	166.84	4.51	146.84	124
	Null	180.99	18.67	178.99	133
	Habitat	181.27	18.95	177.27	132
produced leaves	Habitat × lineage	4104.4	**0**	3360.6	137
	Habitat + lineage	6314.754	2209.922	5578.5	166
	Lineage	6373.811	2268.979	5639.6	167
	Habitat	7093.599	2988.767	6365.4	170
	Null	7137.699	3032.866	6411.5	171
damaged leaves	Habitat × lineage	2698.6	**0**	2091.1	137
	Habitat + lineage	3032.9	334.2867	2433.4	141
	Lineage	3137.2	438.55	2539.6	142
	Habitat	3302.3	603.66	2710.7	145
	Null	3433	734.36	2843.4	146

Models are ranged from the best (ΔAIC = 0) to poorest fits. Bold font denotes models with equivalent empirical support (within 2 AIC units). Residual deviance and residual degrees of freedom are given for each model

Licania (e.g., *Licania* saplings flush light white leaves, Lamarre personal observation). However, these strategies commonly exhibited in tropical tree species (Kursar and Coley 1992) have a high cost for both energy-and nitrogen for the plant (e.g., rubisco production), and continuous producers might have evolved other cost-effective defenses or means to reduce impact of natural enemies.

Phenology of host plant and natural enemies

In our study, we found contrasting responses among species in the correlation between the timing of insect herbivory and leaf production (Figs. 2, 3; Table 1). All species showed an elevated number of positive lags between LPR and HR, except for *M. guyanensis*. In addition, within each lineage, the proportion of positive lags was higher for TF than WS species. In this way, peaks in leaf production appear to be tracked by insects, which consequently produce more damage during the peak of synchronous flush (Fig. 1). This link between the timing of host plant production and herbivores consumption seems to be more common in high-resource habitats (Table 1). However, given limited replications of habitat type in our study, we may not be able to form general conclusions with regards to the effect of habitat on synchrony and thus we recommend further research with repeated measurement across habitats and over multiple seasons.

Previous studies showed that plant growth in the *terra firme* specialists exhibited both greater height and leaf area than white-sand forest specialists (Fine

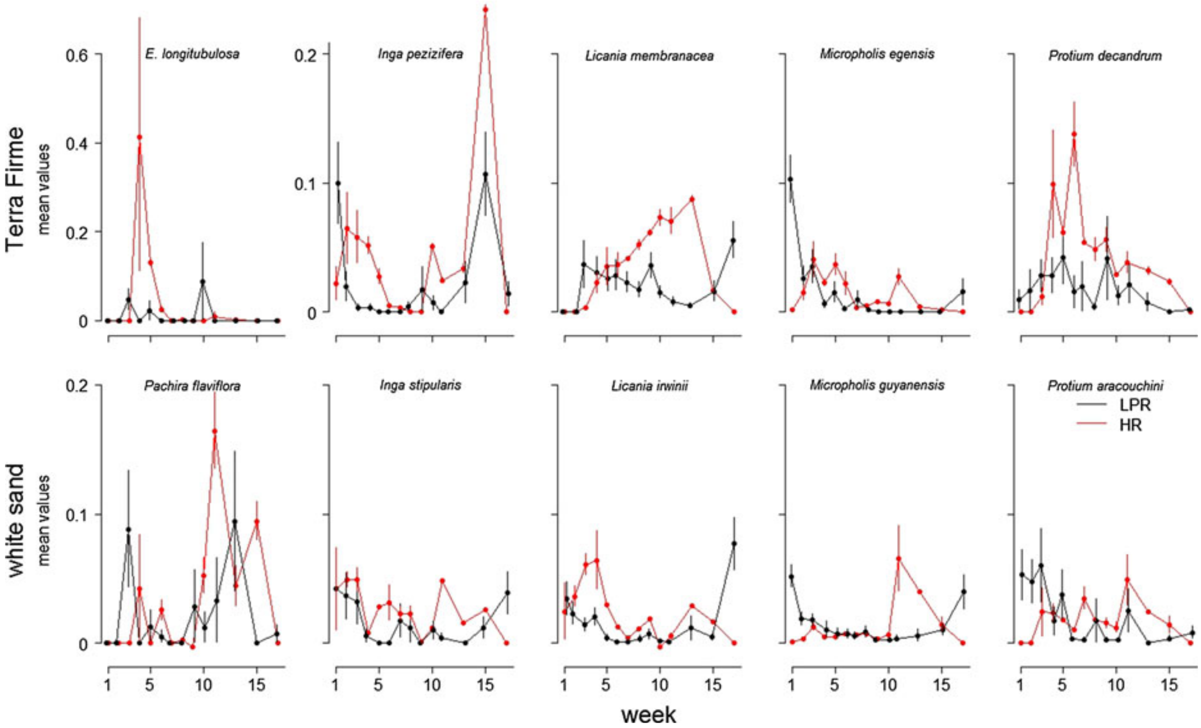

Fig. 2 Plot illustrating the mean values per weeks of the indices of herbivory rate (HR) and leaf production rate (LPR) among the ten studied species during the observation period. *Vertical bars* show standard errors. The *top panels* represent the *terra firme* specialists and the *bottom panels* represent white-sand specialists

et al. 2004), with significantly more leaves produced in high-resource habitats (Lamarre et al. 2012). One potential explanation of tight tracking of changes in LPR by herbivores may be that high-resource habitats support a greater abundance of insect herbivores than low-resource habitats because of a higher turnover of plant tissues (see Fine et al. 2013). For all species except *P. aracouchini* and *M. guyanensis*, the average lag between the peak of leaf production and insect herbivory was lower than 2 weeks, which indicates a very tight tracking by insects (Table 1; Fig. 3). We interpret this result as strong evidence that saplings may minimize the window of leaf expansion when their leaves are most vulnerable (i.e., thinner and more nutritious leaves). The average leaf expansion rate for these species was less than 6 weeks during the study period. This pattern is in agreement with an "escape defense syndrome" that consists of a rapid leaf expansion and synchronous leaf production (see Coley and Kursar 1996; Kursar and Coley 2003).

For the most synchronous tree species, we discern a very close tracking of leaf production by insects as the positive lag between peak of LPR and HR was shorter than the other studied species. For *Protium decandrum* (TF) and *Pachira flaviflora* (WS), 64 and 62 % of the population received intense herbivory rate in less than 2 weeks, respectively. In this way, tight tracking of leaf production by insects may actually favor an indirect defense strategy to reduce their impact (Aide 1991, 1993; van Schaik et al. 1993). A comparable pattern was observed among the ten most synchronous species in a lowland Panamanian forest showing higher herbivory damage occurring after the peak of synchronized flushes (Aide 1993). We suggest that plant species may produce leaves in times of low insect abundances, presumably with the purpose of escaping herbivores. An increase of herbivory during a synchronous flush (or in a short time lag) would suggest that insect herbivores are concentrated in time and space. Thus, insect herbivores would experience satiation if they are not able to completely consume

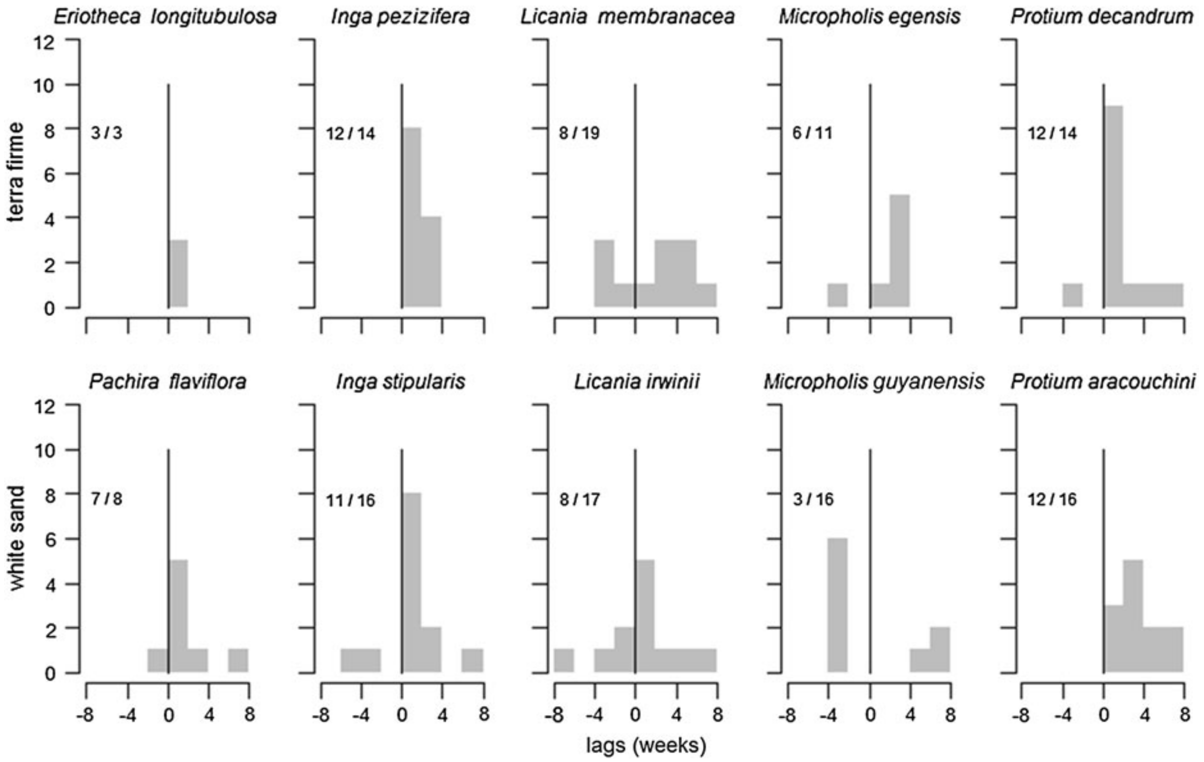

Fig. 3 Histogram of the lags that significantly maximized the cross-correlation among LPR and HR for each species. Positive lags mean that the peak of HR was reached after the peak of LPR and negative lags mean the opposite. The *x*/*y* ratio in the top of each panel means the number of significantly positive cross-correlations in relation with the number of individuals of each species that at least produced a new leaf. The *top panels* represent the *terra firme* specialists and the *bottom panels* represent white-sand specialists

the available resource. Because of a tight tracking of leaf production by insects in addition to a peak of maximum consumption, we hypothesized that the most synchronous species in our study would satiate their herbivore populations. However, we may not have observed satiation events because of the relatively short duration of our monitoring.

Leaf synchrony becomes a viable defense strategy when herbivores are primarily host specialists, and the extent of host specialization for tropical plants is currently unknown (see Novotny et al. 2006). Future long-term studies should focus on natural enemy identities and host preferences to investigate whether specialist insects and resource availability select for divergent patterns of leafing synchrony across a range of availability of resources. The extent to which herbivore specialists may drive the evolution of life history traits such as leafing phenology remains an important question in plant population ecology (van Asch and Visser 2007), and especially in tropical forests where biotic interactions are believed to play a more important role on the rate of speciation than in temperate forests (Schemske et al. 2009).

Conclusion

Our study represents one of the few attempts to measure simultaneously both leaf production and herbivory rates on tropical plants (but see Aide 1993), and to our knowledge is the first to employ a lineage-based approach across a gradient of environmental conditions. Our weekly measurement of leaf production and herbivory allowed us to observe close tracking of leaf production by insects, especially for the most synchronous species, which emphasizes the need for high-precision measurements in plant phenology monitoring (e.g., Aide 1993). This study underlines the importance of considering defense strategies such as the synchrony of leaf production that permits herbivore escape, when studying growth defense tradeoffs across environmental gradients, although it seems to be more dependent on phylogenetic constraints and other environmental cues than soil-derived habitat types.

Acknowledgments We thank Eléonore Bernardo, Jocelyn Cazal, Jean-Yves Goret, and Antonin Leclercq for help in field work. This manuscript has been improved by the help of Q. Molto, P.-C. Zalamea, and C.E.T. Paine. Research was supported by a collaborative NSF Grant (DEB-0743103/0743800) to C. Baraloto and P.V.A. Fine, the Fond Social Européen (FSE) to G.P.A. Lamarre, and an INRA Package Grant to C. Baraloto. I. Mendoza benefited of a Brazilian CNPq Grant (150483/2012-0) during the writing of this paper. This work has benefited from an "Investissement d'Avenir" grant managed by Agence Nationale de la Recherche (CEBA, ref. ANR-10-LABX-25-01). This article is an output of the interaction held during the ATBC meeting in Bonito (June 2012).

References

Agrawal AA, Fishbein M, Halitschke R, Hastings AP, Rabosky DL, Rasmann S (2009) Evidence for adaptive radiation from a phylogenetic study of plant defenses. Proc Natl Acad Sci USA 106:18067–18072

Aide TM (1988) Herbivory as a selective agent on the timing of leaf production in a tropical understory community. Nature 336:574–575

Aide TM (1991) Synchronous leaf production and herbivory in juveniles of *Gustavia superba*. Oecologia 88:511–514

Aide TM (1992) Dry season leaf production: an escape from herbivory. Biotropica 24:532–537

Aide TM (1993) Patterns of leaf development and herbivory in a tropical understory community. Ecology 74:455–466

Augspurger CK (1983) Phenology, flowering synchrony, and fruit-set of six neotropical shrubs. Biotropica 15:257–267

Baraloto C, Rabaud S, Molto Q, Blanc L, Fortunel C, Herault B, Davila N, Mesones I, Rios M, Valderrama E, Fine PVA (2011) Disentangling stand and environmental correlates of aboveground biomass in Amazonian forests. Glob Change Biol 17:2677–2688

Baraloto C, Molto Q, Rabaud S, Hérault B, Valencia R, Blanc L, Fine PVA, Thompson J (2013) Rapid simultaneous estimation of aboveground biomass and tree diversity across Neotropical forests: a comparison of field inventory methods. Biotropica 45:288–298

Becerra JX (1997) Insects on plants: macroevolutionary chemical trends in host use. Science 276:253–256

Bixenmann RJ, Coley PD, Kursar TA (2013) Developmental changes in direct and indirect defenses in the young leaves of the Neotropical tree genus *Inga* (Fabaceae). Biotropica 45:175–184

Bolker BM, Brooks ME, Clark CJ, Geange SW, Poulsen JR, Stevens MHH, White JSS (2009) Generalized linear mixed models: a practical guide for ecology and evolution. Trends Ecol Evol 24:127–135

Bonal D, Bosc A, Ponton S, Goret J-Y, Burban B, Gross P, Bonnefond J-M, Elbers J, Longdoz B, Epron D, Guehl J-M, Granier A (2008) Impact of severe dry season on net ecosystem exchange in the Neotropical rainforest of French Guiana. Glob Change Biol 14:1917–1933

Burnham KP, Anderson DR (1998) Model selection and inference: a practical information theoretic approach. Springer, New York

Coley PD (1980) Effects of leaf age and plant life-history patterns on herbivory. Nature 284:545–546

Coley PD, Kursar TA (1996) Anti-herbivore defenses of young tropical leaves: physiological constraints and ecological tradeoffs. In: Mulkey SS, Chazdon R, Smith AP (eds) Tropical forest plant ecophysiology. Springer, Berlin, pp 305–337

Coley PD, Bryant JP, Chapin FS (1985) Resource availability and plant antiherbivore defense. Science 230:895–899

Ehrlich PR, Raven PH (1964) Butterflies and plants: a study in coevolution. Evolution 18:586–608

Feeny P (1976) Plant apparency and chemical defense. In: Wallace J, Mansell R (eds) Biochemical interaction between plants and insects. Springer, Berlin, pp 1–40

Fine PVA, Mesones I, Coley PD (2004) Herbivores promote habitat specialization by trees in amazonian forests. Science 305:663–665

Fine PVA, Miller ZJ, Mesones I, Irazuzta S, Appel HM, Stevens MHH, Saaksjarvi I, Schultz LC, Coley PD (2006) The growth defense trade-off and habitat specialization by plants in Amazonian forests. Ecology 87:S150–S162

Fine PVA, Metz MR, Lokvam J, Mesones I, Zuniga JMA, Lamarre GPA, Pilco MV, Baraloto C (2013) Insect herbivores, chemical innovation, and the evolution of habitat specialization in Amazonian trees. Ecology 94:1764–1775

Fortunel C, Paine CET, Fine PVA, Kraft NJB, Baraloto C (2014) Environmental factors predict community functional composition in Amazonian forests. J Ecol 102:145–155

Hanley ME, Lamont BB, Fairbanks MM, Rafferty CM (2007) Plant structural traits and their role in anti-herbivore defence. Perspect Plant Ecol Evol Syst 8:157–178

Heil M, Kost C (2006) Priming of indirect defences. Ecol Lett 9:813–817

Herms DA, Mattson WJ (1992) The dilemma of plants: to grow or defend. Q Rev Biol 67:283–335

Kursar TA, Coley PD (1992) Delayed greening in tropical leaves: an antiherbivore defense. Biotropica 24:256–262

Kursar TA, Coley PD (2003) Convergence in defense syndromes of young leaves in tropical rainforests. Biochem Syst Ecol 31:929–949

Lamarre GPA, Baraloto C, Fortunel C, Davila N, Mesones I, Grandez Rios J, Rios M, Valderrama E, Vasquez Pilco M, Fine PVA (2012) Herbivory, growth rates, and habitat specialization in tropical tree lineages: implications for Amazonian beta-diversity. Ecology 93:S195–S210

Legendre P, Legendre L (1998) Numerical ecology. Elsevier, Amsterdam

Lieberman D, Lieberman M (1984) The causes and consequences of synchronous flushing in a dry tropical forest. Biotropica 16:193–201

Macauley BJ, Fox LR (1980) Variation in total phenols and condensed tannins in *Eucalyptus*: leaf phenology and insect grazing. Aust J Ecol 5:31–35

Marquis RJ (1984) Leaf herbivores decrease fitness of a tropical plant. Science 226:537–539

McKey D (1975) The ecology of coevolved seed dispersal systems. In: Gilbert LE, Raven PH (eds) Coevolution of plants and animals. University of Texas, Austin, pp 159–191

McKey D (1989) Interactions between ants and leguminous plants. In: Stirton CH, Zarucchi JL (eds) Advances in legume biology. Monographs in Systematic Botany from the Missouri Botanical Garden, vol 29, pp 673–718

Molino JF, Sabatier D, Prévost MF, Frame D, Gonzalez S, Bilot-Guérin V (2009) Etablissement d'une liste des espèces d'arbres de la Guyane française. IRD, Cayenne

Mooney KA, Halitschke R, Kessler A, Agrawal AA (2010) Evolutionary trade-offs in plants mediate the strength of trophic cascades. Science 327:1642–1644

Novotny V, Drozd P, Miller SE, Kulfan M, Janda M, Basset Y, Weiblen GD (2006) Why are there so many species of herbivorous insects in tropical rainforests? Science 313:1115–1118

Pennec A, Gond V, Sabatier D (2010) Tropical forest phenology in French Guiana from MODIS time series. Remote Sens Lett 2:337–345

Pennington TD, Gasson P, Hanson L, Kite G, Harborne J (1997) The genus *Inga*: botany. Royal Botanic Gardens, Richmond, UK, 844 pp

Poorter L, Bongers L, Bongers F (2006) Architecture of 54 moist-forest tree species: traits, trade-offs, and functional groups. Ecology 87:1289–1301

R Development Core Team (2012) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna

Schemske DW, Mittelbach GG, Cornell HV, Sobel JM, Roy K (2009) Is there a latitudinal gradient in the importance of biotic interactions? Annu Rev Ecol Evol Syst 40:245–269

van Asch M, Visser ME (2007) Phenology of forest caterpillars and their host trees: the importance of synchrony. Annu Rev Entomol 52:37–55

van Schaik CP, Terborgh JW, Wright SJ (1993) The phenology of tropical forests: adaptive significance and consequences for primary consumers. Annu Rev Ecol Syst 24:353–377

Wagner F, Rossi V, Stahl C, Bonal D, Hérault B (2013) Asynchronism in leaf and wood production in tropical forests: a study combining satellite and ground-based measurements. Biogeosci Discuss 10:8247–8281