Ecology

Differential herbivory and successional status in five tropical tree species

Herbivoría diferencial y estatus sucesional en cinco especies de árboles tropicales

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Abstract

Using 4 restoration plots, we performed a common garden experiment to test the hypothesis that inter-specific variation in leaf herbivory depends on the successional status of tree species of the seasonally dry tropical forest. In July of 2011, we calculated the standing levels of herbivory in 5 species at the beginning of the rainy season: *Ipomoea pauciflora* (early-successional), *Swietenia humilis*, and *Pseudobombax ellipticum* (intermediate-successional) and *Jacaratia mexicana* and *Bursera linanoe* (late-successional). From each individual tree, we selected 14 leaves to measure herbivory (N = 84 plants, 821 leaves). The mean leaf area lost by herbivory across the 5 tree species was 5.25%. The results evidencing differences among the categories evaluated supported our hypothesis, as herbivory increased from the late to the early-successional species. We discussed the proximate (i.e, differential leaf traits) and ultimate causes (i.e., differential selective pressures) operating on trees situated at the extreme of the successional stages that could explain the inter-specific differences in herbivory we observed. In accordance with our results, successional status should be recognized as a factor affecting herbivory in tree species in tropical dry forests.

Keywords: Common garden experiment; Early and late succession; Foliar damage; Insect herbivory; Life-history; Restoration plantings; Seasonally dry tropical forest

Resumen

Usando 4 parcelas de restauración, implementamos un experimento de jardín común para evaluar la hipótesis de que la variación interespecífica en la herbivoría foliar se relaciona con el estado sucesional de los árboles del bosque tropical estacionalmente seco. En julio de 2011, calculamos los niveles de herbivoría en 5 especies al inicio de la época lluviosa: *Ipomoea pauciflora* (sucesión temprana), *Swietenia humilis* y *Pseudobombax ellipticum* (sucesión intermedia)

y *Jacaratia mexicana* y *Bursera linanoe* (sucesión tardía). De cada planta, seleccionamos aleatoriamente 14 hojas para medir la herbivoría (N = 84 plantas, 821 hojas). El promedio de área foliar perdida por herbivoría en las 5 especies de árboles fue 5.25%. Los resultados indicaron diferencias entre las categorías evaluadas que apoyaron nuestra hipótesis, mostrando que la herbivoría incrementó de las especies de sucesión tardía a las de sucesión temprana. Discutimos sobre las causas próximas (i.e., características foliares distintas) y últimas (i.e., presiones selectivas distintas) que operan sobre árboles pertenecientes a los extremos de las categorías sucesionales que podrían explicar las diferencias que observamos en los niveles de herbivoría. De acuerdo con los resultados, el estado sucesional debe reconocerse como un factor que afecta la herbivoría en especies de árboles en bosques tropicales secos.

Palabras clave: Experimento de jardín común; Sucesión temprana y tardía; Daño foliar; Herbivoría por insectos; Historia de vida; Parcelas de restauración; Bosque tropical estacionalmente seco

Introduction

Several hypotheses have been posed to explain the concurrent observation about differences in the amount of tissue lost by insect herbivores by different groups of plants (Bryant et al., 1983; Coley et al., 1985; Herms & Mattson, 1992; Johnson, 2011; Stamp, 2003). Empirical evidence and theoretical models indicate that both, susceptibility of plants to be consumed, as well as the response of plants to herbivory (i.e., evolution of resistance or tolerance to damage), are related with resource availability (Bryant et al., 1983; Hawkes & Sullivan, 2001; Hilbert et al., 1981; Maschinski & Whitham, 1989).

Bazzaz (1979) proposed that variation in physiological and life-history traits is expressed along the successional status of species. At a one extreme, late-successional species, corresponding to those chronically subjected to limiting availability of resources display traits that enhance fitness prioritizing permanence. Late-succesial species generally express slow growth, higher allocation to defense and consequently tend to exhibit low levels of herbivory. At the other extreme, higher resource allocation to growth instead of defense is expected in species evolving in more favorable conditions; therefore, early-successional species accumulate damage at higher rates (Coley, 1983; Coley et al., 1985; Fine et al., 2006).

In specific, several studies provided abundant evidence on the relationship between variation in growth rates and successional status in seasonally dry tropical forest species (Álvarez-Aquino & Williams-Linera, 2012; Foroughbakhch et al., 2006; Huante & Rincón, 1998; Kalacska et al., 2004; Lebrija-Trejos et al., 2010; Rincón & Huante, 1992 Soriano et al., 2011). However, studies incorporating the effect of successional status as a likely factor explaining inter-specific differences in herbivory in tropical dry forests are scarce (Table 1). Thus, as far as we know, studies addressing how successional stages are related to herbivory in restoration plantings within seasonally dry tropical forests are not available. Restoration plantings could represent scenarios for the implementation of common-garden experiments, which are useful to explore the occurrence of inherent differences in the pattern of herbivory, as they provide similar environmental conditions for different tree species. Regarding herbivory, for example, it can be expected that groups of tropical tree species growing simultaneously in homogeneous conditions, should express variation in the susceptibility to herbivory related to differences in successional status (Massad et al., 2011). In this study, we predict differential herbivory in tree species growing in a seasonally dry forest located in Central Mexico. Assuming that plants within the plots are exposed to a similar environment (i.e., edaphic conditions, light regime, water availability and density of insect herbivores), herbivory is expected be greater in early-successional tree species than in late-successional species.

Materials and methods

The study site is located within the Sierra of Huautla Biosphere Reserve nearby the town El Limón de Cuauchichinola. The reserve includes a large portion of the state of Morelos, Mexico nearby the states of Guerrero and Puebla (18°20'10"-18°34'20" N, 98°51'20"-98° 08'15" W). The original vegetation in this area corresponded to seasonally dry tropical forest. After being used for maize cultivation, extensive areas of old-fields were abandoned around 30 years ago. Currently, the Reserve is a mosaic of original vegetation present in ravines and hills, which are surrounded by secondary vegetation and flatter areas heavily transformed to agricultural lands (Martínez-Garza et al., 2011).

As a part of a previous experiment, in January of 2006, 8 restoration plots (50 × 50 m) were fenced to exclude livestock and extraction of plants and the animals by the local people. At each plot, all the originally present trees [≥ 5 cm diameter at breast height (dbh = 1.3 m)] were tagged and measured, recording 33 woody species from 14

Table 1

Herbivory measurements in tree species of the seasonally dry tropical forest. Herbivory is presented as the mean percentage of area eaten (% AE). The minimum and maximum (min-max) indicate extreme values reported per species. Values of %AE marked with * were derived from figures; those marked with ** were calculated from supplementary material. Non-marked values were directly provided by authors in the text. Information about if the studies included criterions as phenology (D, deciduous / E, evergreen) or successional stages (E, early; I, intermediate or L, late succesional) is provided.

Site	N	(% AE)	Min-max 26.14-30.81	Phenology	Successional stage	Reference
Chamela, Jalisco	12	7.57	1.56-19.53	No	No	Filip et al., 1995
Dzibilchaltún, National Park region, Yucatán	3	3.65 *	2.45-4.65	D	No	Campo & Dirzo, 2003
Chamela, Jalisco	3	14.85 *	12.4-17.3	D	No	Boege, 2004
Chamela, Jalisco	23	11.5 **	0.6-28.2	D/E	No	Pringle et al., 2011
Chamela, Jalisco	2	21.65	9.9-33.4	D	No	Hernández et al., 2014
RBSH, Morelos	2	28.47	26.14-30.81	D	E	Juan-Baeza et al., 2015
Minas Gerais, Brazil	31	6.5 *	–	No	No	Neves et al., 2010
Mata Seca State Park, Minas Gerais	1	8.63 *	6.0-10.8	D	E, I, L	Silva et al., 2012
Minas Gerais, Brazil	–	5.36 *	3.5-7.8	D	E, I, L	Neves et al., 2014

families (density of 252.5 trees/ha; basal area of 6.18 m^2/ha; Martínez-Garza et al., 2011). At that moment, the most abundant species were *Acacia cochliacantha* (Fabaceae, 75 trees/ha), *Ipomoea pauciflora* (Convolvulaceae, 50 trees/ha) and *Mimosa benthamii* (Fabaceae, 31 trees/ha). To experimentally facilitate natural succession, 4 of these plots were enriched with seedlings (ca., 40 cm height) of 20 native tree species (Carrasco-Carballido & Martínez-Garza, 2011). In July of 2011, we used the enriched plots of that restoration experiment to test the effect of successional status on the standing levels of herbivory in 5 tree species, which included those species that had foliage starting this study. One naturally established tree species, *Ipomoea pauciflora* M. Martens & Galeotti (Convolvulaceae) and 4 planted native species, *Bursera linanoe* (La Llave) Rzed., Calderón & Molina, *Jacaratia mexicana* A. DC. (Caricaceae), *Pseudobombax ellipticum* (Kunth) Dugan (Bombacaceae) and *Swietenia humilis* Zucc. (Meliaceae), were used for this study.

According to the literature, the 5 species were assigned to early, intermediate or late successional status (Table 2). *I. pauciflora* is considered an early successional tree species given its fast growth rates with high availability of resources (Huante et al., 1995) and higher density in early successional environments (Martínez-Garza et al., 2011). *P. ellipticum* and *S. humilis* were considered intermediate-successional species given their growth rates which are lower than those of early successionals (Huante et al., 2012). *Bursera* species (Rzedowski & Kruse, 1979) and

Jacaratia mexicana (Bullock, 2002) are usually found only at late-successional stages (Table 2).

Leaf herbivory was evaluated during July 2011 (2 to 5 plants per species per plot at 4 plots; N = 84 plants). From each individual tree, we randomly selected 14 leaves to measure herbivory (N = 821 leaves). Leaves were not collected to avoid a possible impact on survivorship and growth of plants. The amount of insect damage of each individual leaf was assigned to one of 6 categories considered by Dirzo and Domínguez (1995): the category 0 represents leaves without damage (0%). The other 5 categories represent ranges of damage, as follows: 1 = 1-6%, 2 = 7-12%, 3 = 13-25%, 4 = 26-50%, 5 = 51-100%. Following Dirzo and Domínguez (1995), we calculated the index of herbivory as follows: $H = \Sigma (C_i \times n_i) / N$, where C_i is the category of damage, n_i is the number of leaves that present damage of a given category and N is the total number of leaves.

To evaluate the effect of successional status on the level of herbivory, we used a mixed-effects model based on restricted maximum likelihood estimation of parameters. As a surrogate of the successional status (i.e., early, intermediate and late-successional), an ordered fixed factor was adopted. Species identity nested within site was specified as a random component. We tested for the presence of linear and quadratic relationships of the ordered fixed factor on damage, using a polynomial contrast. In addition, we used a different mixed-effects model to test the effect of tree species on herbivory.

Table 2

Families, seed weight (mg), successional status and references that support classification of successional status of 5 dry forest tree species in experimental restoration plots in El Limón de Cuauchichinola, Sierra de Huautla, Morelos, Mexico.

Species	Family	Seed weight	Succesional status	Reference
Ipomoea pauciflora	Convolvulaceae	86.40*	Early	Huante et al., 1995 Martínez-Garza et. al., 2011
Swetenia humilis	Meliaceae	50.00*	Intermediate	Huante et al., 2012
Pseudobombax ellipticum	Bombacaceae	69.46*	Intermediate	Almazán-Núñez et al., 2012
Bursera linaloe	Burseraceae	58.74**	Late	Rzedowski & Kruse, 1979 Beltrán-Rodríguez et al., 2018
Jacaratia mexicana	Caricaceae	516.13*	Late	Bullock, 2002 Lebrija-Trejos et al., 2010

* Kattge et al. (2011); ** Mendoza-Segovia (2017)

We defined species identity as a fixed factor, whereas we specified the effect of site as a random component. We evaluated inter-specific differences between mean values of herbivory using the Tukey HSD post hoc test. For both mixed models, the index of herbivory per plant was square root-transformed to fulfill model assumptions of normality and homoscedasticity of residuals. For clarity, in all cases we reported mean and standard error values of untransformed data. All statistical analyses were carried out using R 3.2.3 (R Core Team, 2015). We fitted linear mixed effects models using the lme function in R (Pinheiro et al., 2015), and *glht* function in library *multcomp* to perform Tukey HSD test (Hothorn et al., 2008).

Results

The mixed-effects model analysis of variance showed that the effect of successional status was significant ($F_{(2, 14)} = 49.56$, $p < 0.001$) and accounted for 69% of the total variance of observed herbivory rates. Polynomial contrasts showed a negative linear tendency between the level of herbivory and successional status ($t_{(14)} = 9.9$, $p < 0.001$). In contrast, quadratic tendency was not statistically significant ($t_{(14)} = 0.72$, $p = 0.4833$). Results indicate that herbivory was greater in the early-successional species, followed by intermediate-successional species and lowest in late-successional species. The early-successional species held 2.5 and 6 times more damage, than intermediate and late-successional species, respectively (Fig. 1).

The effect of tree species identity on herbivory was also statistically significant ($F_{(4, 76)} = 70.82$, $p < 0.001$), and accounted for 78% of total variance. Herbivory in *I. pauciflora* was higher than the observed for *B. linanoe* (Tukey HSD, $p < 0.001$, Fig. 2). *Jacaratia mexicana* had significant lower damage than *S. humilis* (Tukey HSD,

$p = 0.0042$). Herbivory in *P. ellipticum,* was statistically similar to the observed in *J. mexicana* (Tukey HSD, $p = 0.369$) and in *S. humilis* (Tukey HSD, $p = 0.325$) (Fig. 2). Overall, the mean leaf area lost by herbivory across the 5 tree species included in our study was 5.25%, (ranging from 0.5% to 20%).

Discussion

The mean leaf area lost by herbivory across the 5 tree species included in our study was located within the range of results reported for other tree species in Mexico, in
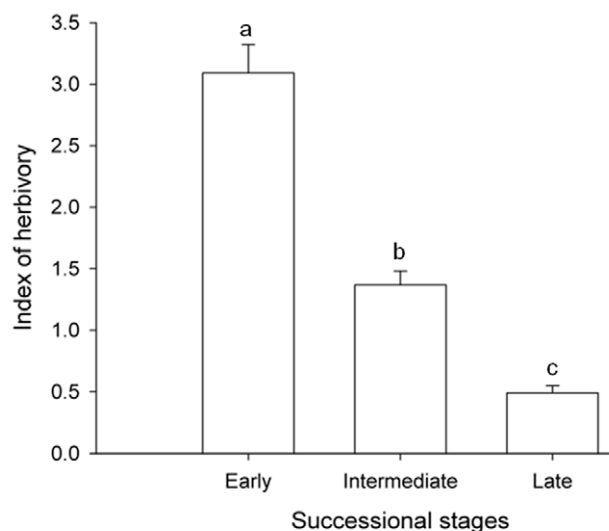

Figure 1. Index of herbivory in early, intermediate and late successional tree species of a dry tropical forest in Mexico (untransformed means ± 1 standard errors are shown, different letters indicate significant differences $p < 0.01$).

which mean percentages of herbivory varied from 3.65 to 28.47 (Table 1). Our mean value was also located within those reported for tropical dry forests in South America (Table 1), and it was very similar to the median value reported by Dirzo and Boege (2008) for tree species of tropical dry forests around the world.

Herbivory and successional status. With regard the effect of the successional status, the evidence derived from this study supported our prediction, as we showed that herbivory increased from the late-successional to the early-successional species. These results can be explained by proximate and ultimate causes. Regarding the functional explanations that occur at the ecological level, it is known that inter-specific differences in herbivory frequently result from comparisons of correlations between defensive foliar characteristics with leaf damage (Coley, 1983, 1987). For example, low levels of herbivory are observed in species whose foliage exhibits higher toughness and pubescence and a higher concentration of fiber, cellulose and secondary metabolites (i.e., tannins, phenols). These characteristics in conjunct are hypothesized to reduce palatability and digestibility of leaf tissue. In contrast, higher herbivory is found in species with the opposite pattern for leaf traits (Coley, 1983, 1987). Interestingly, these differences are not only patent among tree species; but they are also expressed along leaf ontogeny, in which higher allocation to defense and lower herbivory occur in older than in younger leaves (Coley, 1980). Thus, inter-specific variation in traits such as secondary metabolites, nutritional quality and/or leaf toughness could be considered as proximate explanations to the variation in herbivory among tropical tree species. On the other hand, ultimate causes explaining the inter-specific variation in leaf damage are linked with the hypothesis that tropical tree species face differential selective pressures according with the availability of resources to which they are exposed. In consequence, plant species display distinct adaptive life-history traits in contrasting conditions of resource availability, such as those occurring along successional stages (Bazzaz, 1979; Bryant et al., 1985; Coley et al., 1985; Endara & Coley, 2011). For example, a higher resource allocation to growth and higher ability to compensate leaf loss should be advantageous in early-successional species. Consequently, a lower investment on defense is predicted in this group of species. Overall, the evidence available for tropical trees supports a pattern in which, on the one hand, leaves of early-successional species exhibit lower amounts of chemical compounds, foliar toughness, trichome density and higher levels of herbivory. In contrast, the rate of herbivory should be lower in late-successional species, which are exposed to limited resources. Under conditions of stress the ability to compensate the loss of foliage is limited, thus late-successional species tend to increase the allocation of resources to defensive strategies (Coley, 1980, 1983, 1987; Coley et al., 1985).

Herbivory in restoration plots. Reciprocal transplant experiments have been useful to obtain evidence supporting differential adaptive evolution of life-history traits and defensive strategies among groups of tree species. Such experimental approaches showed evidence that the expression of traits involved in growth or defense in plants has a genetic basis (Fine et al., 2004, 2006). Our results supported the expected pattern of herbivory in which level of damage is related to the successional stage of tree species. This is because the differential pattern of leaf damage exhibited among trees belonging to different successional status growing in homogeneous conditions indicates that species exhibit inherent differences in their susceptibility to herbivory (Poorter et al., 2004). Based on our experimental design and the small size of plots, it can be assumed that plant species of different successional status were exposed to similar edaphic and light conditions, as well as to similar herbivore abundance. Thus, although in this study, foliar traits were not measured, we infer that differences in intrinsic characteristics of plants explain the pattern of herbivory we observed (Coley, 1987; Coley et al., 1985; Poorter et al., 2004). In fact, as leaf characteristics correlate with growth rates, foliar traits have been utilized to predict the performance of tropical species to be selected for restoration plantings (Martínez-Garza et al., 2005, 2013).

We considered that the overall mean value of herbivory was not influenced by the occurrence of plants in restoration plots (i.e, a high density of plants). This is because
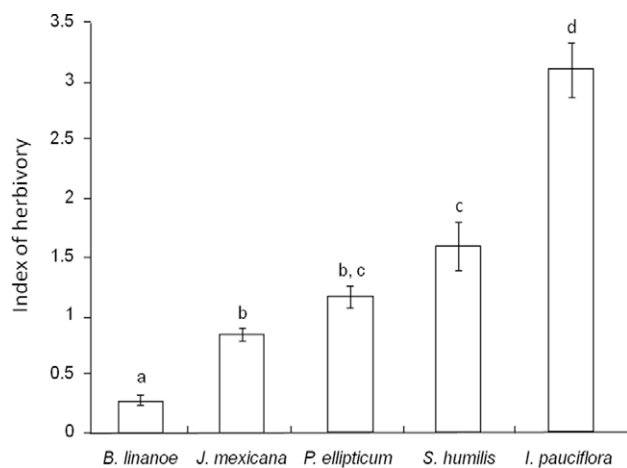

Figure 2. Index of herbivory in 5 species of the seasonally dry tropical forest (untransformed means ± 1 standard errors are shown, different letters indicate significant differences $p < 0.01$).

other independent studies performed on the same study system, showed that herbivory levels were statistically similar between successional sites and restored plots (Hernández et al., 2014), or among different restoration treatments (with and without plantings; Juan-Baeza et al., 2015). In turn, the experimental design we used which was based on restoration plantings was successful in demonstrating inherent differences in herbivory correlated with successional status of plants, as it was shown in a large-scale restoration planting in Brazil, in which early-successional species held higher herbivory than late-successional species (Massad et al., 2011).

Species identity and herbivory. The magnitude of herbivory in *I. pauciflora* was 5 times higher that of the mean value obtained for the other 4 species. The index of herbivory scored in this species corresponds to a leaf area loss of about 20%, whereas damage in the other 4 species was between 1 and 6%. *Ipomoea pauciflora* is an early-successional tree species widely associated with disturbed conditions, being very common along roads, in agricultural lands and in secondary vegetation (Juan-Baeza et al., 2015; Martínez-Garza et al., 2011). It is known that *I. pauciflora* maintains a specialized interaction with *Phytodectoidea quatordecimpunctata* Boheman (Chrysomelidae), a beetle that produces a mean foliar damage of 25-30% of the total leaf area (Castro-Jaimez & Mariano, 2011; Juan-Baeza et al., 2015), with some individuals receiving foliar damage corresponding to 50% or higher (N. Mariano per. obs.). Thus, this specialized plant-insect interaction could explain the higher herbivory levels scored in *I. pauciflora*. The level of damage was much lower within the intermediate-successional plants in which damage ranged between 2 and 3% of the total leaf area for *P. ellipticum* and *Swietenia humilis*, respectively. The late-successional tree, *J. mexicana* received 1% of damage, which agrees with the observation of apparent very low herbivory in this dioecious tree (Bullock, 2002). However, in reproductive individuals, a higher herbivory could be expected in male than in female trees (Cepeda-Cornejo & Dirzo, 2010, and references therein). The other late-successional tree, *Bursera linanoe* is frequently found inhabiting pristine dry tropical forests, being a dominant element of this ecosystem (Rzedowski & Kruse, 1979). Our results show that *B. linanoe* received practically no damage, thus herbivory should not be a limiting factor for growth or survivorship of juveniles of this tree species.

The relationship between the levels of herbivory and successional status of plants was determined including individuals of only 5 tree species (those exhibiting foliage at the moment of the study). This could be a limitation, as studies performed at the community level have detected a marked inter-specific component on the variation in herbivory (Filip et al,. 1995), even within phenological categories (i.e., deciduous and evergreen; Pringle et al., 2011). Thus, the prediction of the relationship between successional status with herbivory should be tested including more plant species. Measurements of growth should be also carried out to directly estimate the relationship between herbivory and growth rates. For future studies, herbivory measurement in marked leaves is also recommended as index of herbivory could underestimate insect damage (Filip et al., 1995).

We have utilized a current restoration experiment of a dry tropical forest to carry out an experimental approach useful for the study of the interaction between tropical trees and their herbivores. We focused on plots previously enriched with native trees to implement a common garden experiment. Considering restoration goals, our results indicate that the pattern of herbivory shown in plantings is the expected regarding inter-specific life-history differences. Thus, plantings might restore plant-insect interactions (Juan-Baeza et al., 2015; Solis-Gabriel et al., 2017). Although some tree species in plantings could be exposed to high levels of herbivory, the effect of herbivory at the community level tends to be diminished in plots exhibiting high species richness (Massad et al., 2011). From a more ecological point of view, according to our results, the differential herbivory observed among tree species sharing a common environment, indicates that successional status should be recognized as a factor shaping the interaction between plants and their herbivores in tropical dry forests.

Acknowledgements

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