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## HERBIVORY DAMAGE ON OAK SEEDLINGS AT THE EDGE OF CLOUD FOREST FRAGMENTS

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**Abstract:** Herbivory damage on *Quercus xalapensis* Humb. et Bonpl. seedlings was experimentally determined in two cloud forest fragments (Veracruz, Mexico), one with an abrupt edge (forest contiguous to a one-year old stand), and another with a soft edge (forest contiguous to a 10 year-old stand). Sets of seedlings were planted in transects parallel to the border. The experiments were conducted in the warm-dry (April-May) and warm-wet (July-August) seasons. Herbivory damage was measured at the beginning and at the end of each season. Weekly, microclimatic variables were measured in the same positions in which seedlings were planted. During the wet season, herbivory was similar at different distances from the border (ca. 2%), but during the dry season, herbivory was higher at the forest border (2.75-11.75%) than at the old-field (0.50-0.75%). Herbivory and air temperature were higher, and air humidity and soil water content were lower in the abrupt than in the soft edge. Our results suggest that herbivory levels on oak seedlings depend on modulating factors such as the edge type and the season of the year.

**Key words:** edge effect modulators, forest edges, herbivory, microenvironment, oak seedlings.

**Resumen:** El daño por herbivoría en plántulas de *Quercus xalapensis* Humb. et Bonpl. fue determinado experimentalmente en dos fragmentos de bosque mesófilo de montaña (Veracruz, México), uno con borde abrupto (bosque contiguo a acahual de un año) y otro con borde suave (bosque contiguo a acahual de 10 años). Se sembraron grupos de plántulas en transectos paralelos al borde durante la estación cálida-seca (abril-mayo) y cálida-húmeda (julio-agosto). La herbivoría se midió al inicio y al final de cada estación. Las variables climáticas fueron medidas semanalmente, en los sitios donde se sembraron las plántulas. Durante la estación húmeda, la herbivoría fue similar a diferentes distancias del borde (ca. 2%), pero en la estación seca la herbivoría fue mayor en el borde del bosque (2.75-11.75%) que en el acahual (0.50-0.75%). La herbivoría y la temperatura del aire fueron mayores, y la humedad del aire y del suelo fueron menores, en el borde abrupto que en el suave. Los resultados sugieren que el nivel de herbivoría sobre las plántulas de encino depende de factores moduladores como el tipo de borde y la estación del año.

**Palabras clave:** bordes de bosque, herbivoría, microambiente, moduladores de efecto de borde, plántulas de encino.

Insect herbivores respond to small-scale environmental variables, damaging plants in some locations while others are left undamaged (Meiners *et al.*, 2000). Insect herbivore damage level may be a response to edge creation, but the magnitude (higher or lower) and direction (positive or negative) of the response to the distance from a border is inconsistent. In a Neotropical lowland rain forest in Chiapas, Mexico, biotic damage on seedlings was higher at the edge than in the forest interior (Benítez-Malvido and Lemus-Albor, 2005). In contrast, in a montane forest in

Chiapas, oak seedlings planted in the edge and in the forest suffered more defoliation than those seedlings planted in adjacent open areas (López-Barrera *et al.*, 2006). In a temperate forest in New Jersey, USA, insect herbivore damage to *Quercus rubra* seedlings varied irregularly across an edge gradient 30 m inside the forest to 60 m into the old-field (Meiners and Martinkovic, 2002). However, in the same temperate forest, Meiners *et al.* (2000) reported a higher insect herbivory level at the edge on *Fraxinus americana*, but only during a drought year. Those authors con-

cluded that edges represent complex environmental gradients that limit the invasion and establishment of trees into adjacent old-fields, and that the limitation is correlated with yearly fluctuations in rainfall.

Apparently, forest edge effects are modulated by many factors. Among them, edge type (Ries *et al.*, 2004; or edge contrast *sensu* Harper *et al.*, 2005) is a main modulator on the magnitude and direction of the edge influence. Vegetation structure at edges has an important influence on biotic interactions (Didham and Lawton, 1999; Gehlhausen *et al.*, 2000; Guzmán-Guzmán and Williams-Linera, 2006; López-Barrera *et al.*, 2006). According to development of the vegetation at the forest edge, edges can be characterized as soft or abrupt edges (Harper *et al.*, 2005). At soft edges, woody plant density is higher than at abrupt edges, and acorn removal and seedling mortality are lower in the forest interior and soft border, and higher in old-fields and in the abrupt edge sites (Guzmán-Guzmán and Williams-Linera, 2006). Furthermore, edge penetration distance for microclimate and vegetation structure variables may be two to five times greater at abrupt than at soft edges (Didham and Lawton, 1999). The adjacent community type is important in determining edge effects depth into the forest interior since the extent of microclimatic edge effect is reduced by the presence of a protective border such as the buffering of large trees (Gehlhausen *et al.*, 2000).

Insect herbivore damage may change with distance from a border associated to a microclimatic gradient across forest-old-field. But, modulator factors may determine where or when the edge effect on seedling herbivory will be more apparent. The objective of this study was to determine herbivory damage to oak seedlings in forest edges with contrasting characteristics, and microclimatic changes during a dry and a wet seasons.

## Materials and methods

The study was conducted in the tropical montane cloud forest region of central Veracruz, Mexico. There are three defined seasons: a warm-dry season during April and May, a warm-wet season from June to October, and a relatively cold-dry season from November to March. Temperature and precipitation were obtained from the nearest meteorological station located in Xalapa, *ca.* 5 km from the sites and at similar altitude. During the warm-dry season (April and May, 2003), precipitation was 166 mm, and maximum and minimum mean temperatures were 28 and 16°C, respectively. In contrast, during the warm-wet season (July and August, 2003), precipitation was 287 mm, and maximum and minimum mean temperatures were 27 and 14°C, respectively.

In this area, two forest fragments representing contrasting edges were selected. One site had an abrupt edge, as the forest was contiguous to a one-year-old abandoned field,

and had an eastern orientation (Banderilla, 19°35'N, 96°58'W; 1,450-1,490 m altitude; slope 26-31°, 25 ha). The other site had a soft edge because the forest fragment was adjacent to a 10-year-old stand and had a southern orientation (Tlalnelhuayocan, 19°31'N, 96°58'W; 1,350-1,360 m altitude; slope 30-37°, 5 ha). Fragments are of different sizes and orientations, but that is not crucial for the scale of this study. *Quercus* spp. are the dominant trees in the forest fragments; other abundant tree species are *Carpinus caroliniana* Walter, *Clethra mexicana* DC., *Liquidambar styraciflua* L. var. *mexicana* Oersted, and *Turpinia insignis* (Kunth) Tul.

*Quercus xalapensis* Humb. & Bonpl. was selected for a seedling herbivory study considering its dominance in the cloud forest. *Q. xalapensis* belongs to the *Erythrobalanus* subgenus (red oak) and is a semi-deciduous tree species; in our study area leafing consistently takes place in late February/March, with new leaves beginning to expand well before the majority of old leaves have abscised. Mature acorns are ready in October-November, and after a short latency acorns germinate in January (GWL, unpublished data).

Studied seedlings were obtained from acorns collected from the forest floor underneath several trees and germinated in a greenhouse in the Botanical Garden of the Instituto de Ecología, A.C. The timing of acorn germination in the greenhouse coincided with that in the forest, resulting in similar ages of seedlings transplanted compared to those that germinated naturally in the forest. The shade conditions in the greenhouse were similar to the forest understory, and the same forest soil was used to grow the seedlings. Seedlings were kept in a herbivore-free greenhouse for a couple of months until transplanted into the field; they were randomly separated in two groups.

Field experiments were carried out during the warm-dry and warm-wet seasons. At each study site, seedlings were transplanted into four 50 m-long transects parallel to the forest border. The border (0 m) was defined by the presence of old trees. The transects were: 30 m into the forest interior, forest edge and old-field edge (0-10 m from the border), and 30 m into the old-field. Thirty meters was considered as interior conditions based on previous forest edge studies carried out in the region (Williams-Linera, 1993; Guzmán-Guzmán and Williams-Linera, 2006). Along each transect, four 1 × 1 m plots were marked separated by 10 m from each other. In each plot, five seedlings of *Q. xalapensis* were planted on the first day of April and on the first day of July; each experiment lasted eight weeks. Each seedling was marked with a tag attached to the stem with wire, and each leaf was numbered using an indelible pen.

At the inception of each experiment, to record leaf contour, a photograph of each leaf placed on millimeter square paper was taken with a digital camera Sony MVC-FD73. At the end of each experimental period, all leaves were col-

lected and stored in plastic bags in a refrigerator at 5°C until they were processed. Leaf area and herbivore damage were determined for each leaf using a leaf area meter LI-3100, Li-Cor. We recorded only damage by leaf-chewing insects, and not that generated by leaf miners or gall producers. When leaves were almost completely eaten or lost they were reconstructed using the digital photographs and a computer. First, the remnant leaf area was measured, and second, the missing sections were covered with masking tape and the original or total area was recorded. With these data, percent of leaf damage area was determined as:

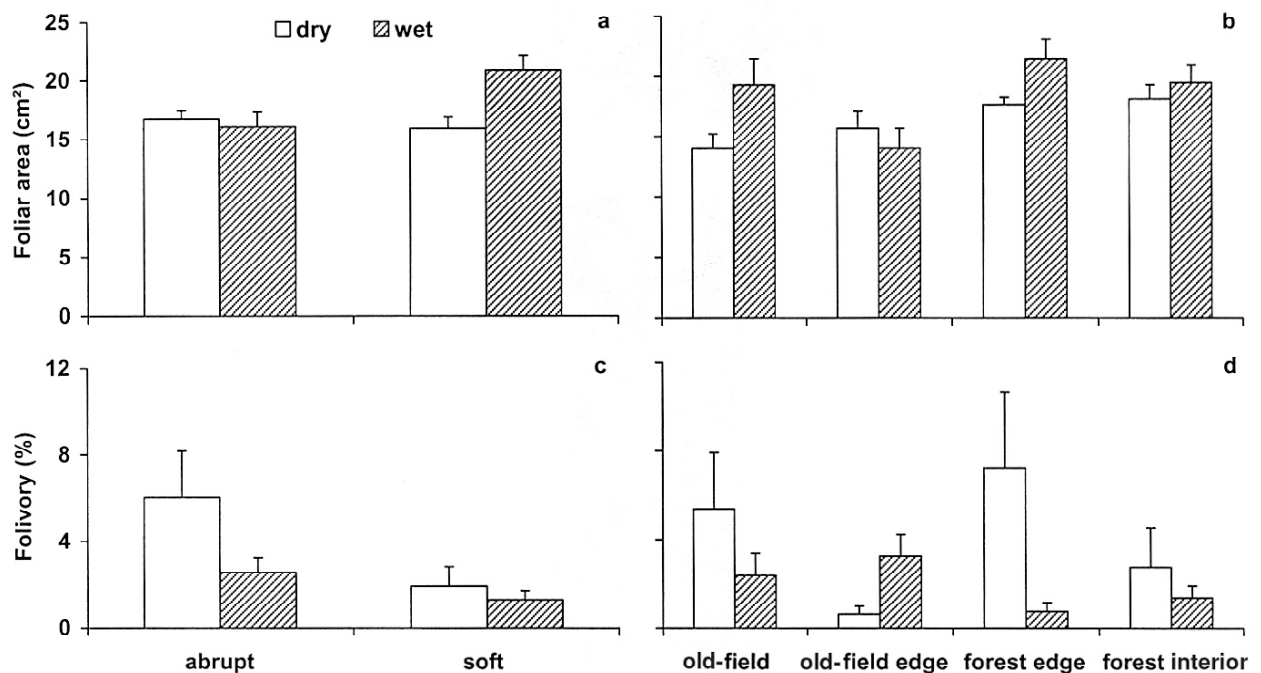
$$\text{Herbivory \%} = (\text{total area} - \text{remnant area}) * 100 / \text{total area}$$

Weekly, from April 1 to August 30, 2003, microclimatic variation was measured at each study site along the same transects in which the oak seedlings were planted. On the same day between 12:00 and 13:00 h, at two locations for each transect, air temperature and relative humidity were measured 1 m above the soil using a digital thermohygrometer, Pen-Type. Soil temperature at 5 cm depth was measured with a thermometer, and soil water content was determined in soil samples collected at 10 cm depth without fresh litterfall. Soil samples were transported to the lab in plastic bags, weighed before and after being oven-dried during 72 h at 70°C.

Data were analyzed using three-way full factorial ANOVAs; response variables were herbivory and microenvironmental variables; sources of variation were season, site, and distance from the border. Prior to analysis, the normality of the data was assessed using the Shapiro-Wilk's test, and transformations were performed when necessary. Percent herbivory averaged per plant was arcsine transformed, and microenvironmental data were log transformed to achieve normality. When significant differences were detected, means were compared using the Tukey-HSD test. Relationships between herbivory and microenvironmental variables were determined using Pearson correlation coefficients. Statistical analyses were done using the statistical package JMP version 3.2.2 (SAS, 1997). Only significant results are reported.

## Results

Survival of oak seedlings was high in the two sites and during both seasons (*ca.* 96%). A total of 1,617 leaves was measured during this study. The significant site  $\times$  season interaction ( $F = 8.35$ , d.f. = 1,  $P = 0.006$ ) indicates a greater leaf area in seedlings growing along the soft edge site, but only during the wet season (figure 1a). There was a significant effect of distance from the border on leaf area ( $F = 4.81$ , d.f. = 3,  $P = 0.005$ ). Leaf area was higher in the seedlings



**Figure 1.** Leaf area (cm<sup>2</sup>) and herbivory (%) of oak seedlings during the dry and wet seasons in abrupt and soft edges (a, c), and old-field, old-field edge, forest edge and forest interior habitats (b, d) in central Veracruz, Mexico. Error bars represent one S.E.

growing along the forest interior and forest edge than in the old-field and old-field edge (figure 1b).

Percent herbivory was higher in the abrupt than in the soft edge site ( $F = 5.92$ , d.f. = 1,  $P = 0.02$ ; figure 1c). A significant distance from the border  $\times$  season interaction ( $F = 3.59$ , d.f. = 3,  $P = 0.02$ ) indicates that percent herbivory was higher at the forest edge and lower at the old-field edge during the dry season, however, during the wet season, herbivory was similar along the forest interior–old-field gradient (figure 1d).

Air and soil temperatures were higher at both sites during the dry than during the wet season ( $F = 9.59$ , 28.12, respectively, d.f. = 1,  $P < 0.0001$ ), and they were higher in the abrupt than in the soft edge site ( $F = 30.88$ , 56.41, respectively, d.f. = 1,  $P < 0.01$ ; figure 2a, b). Air and soil temperatures were higher in the old-field and the old-field edge than in the forest edge and forest interior ( $F = 15.0$ , 46.5, respectively, d.f. = 3,  $P < 0.0001$ ; figure 2e, f).

Percentages of relative humidity and soil water content were higher in the wet than in the dry season ( $F = 16.4$ , 62.8, respectively, d.f. = 1,  $P < 0.01$ ), and higher in the soft than in the abrupt edge site ( $F = 47.0$ , 9.5, respectively, d.f. = 1,  $P < 0.01$ ; figure 2c, d). Relative humidity was similar in the old-field and old-field edge, and lower there than in the forest edge, whereas relative humidity was higher in the forest interior ( $F = 11.17$ , d.f. = 3,  $P < 0.0001$ ; figure 2g). Soil water content was statistically similar among distances; however, the interaction site  $\times$  season was significant ( $F = 6.1$ , d.f. = 1,  $P = 0.01$ ). During the dry season, the soil water content was higher in the soft edge site. Nevertheless, during the wet season there were no differences between sites. The interaction site  $\times$  distance from the border was significant ( $F = 6.5$ , d.f. = 3,  $P < 0.01$ ) due to higher water content in old-field and edges in the soft edge site (figure 2h).

Herbivory percent was not significantly correlated with air temperature ( $r = -0.40$ ,  $P = 0.12$ ), but it was negatively correlated with relative humidity ( $r = -0.49$ ,  $P = 0.05$ ), and with soil water content ( $r = -0.55$ ,  $P = 0.03$ ).

## Discussion

Although herbivore insect communities associated with oaks are mostly unknown for our study area, we assume that most leaf damage was caused by insects, since large mammalian herbivores are largely extinct in the region, and rodent herbivores typically kill seedlings by clipping stems, and there was no evidence for meteorological induced damage. Invertebrate leaf damage represents an important source of herbivory for *Quercus* seedlings (Le Corff and Marquis, 1999; Guzmán-Guzmán and Williams-Linera, 2006; López-Barrera *et al.*, 2006). In a temperate forest in Missouri, USA, 250 leaf chewing insect species feed on *Quercus alba* and *Q. velutina*, 90% of which are larvae of

Lepidoptera, and the remaining 10% are sawflies, beetles, walking sticks, grasshoppers and katydids (R.J. Marquis, unpublished; cited in Le Corff and Marquis, 1999). In a montane forest in Chiapas, Mexico, López-Barrera *et al.* (2006) reported that the oak seedling defoliation was higher in the forested portion of an old-field–forest interior gradient, and that the pattern was caused by increased herbivory by lepidopteran larvae.

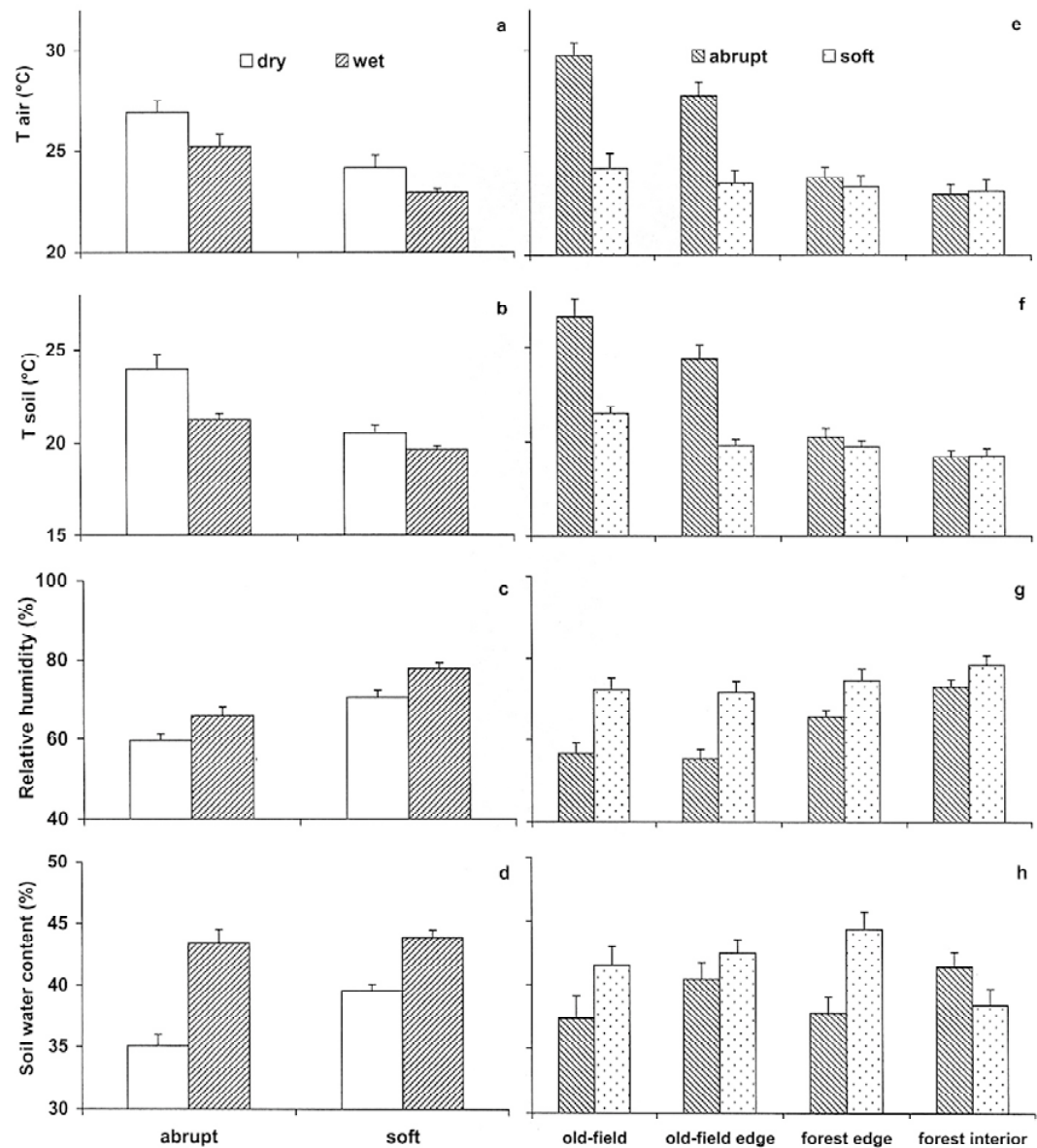
We found similar insect herbivory damage on oak seedlings during the dry (2–6%) and wet (1–3%) seasons in both study sites. In contrast, most of the community-level studies carried out in forest interiors consistently reported the lowest herbivory damage during the dry season (*e.g.* Aide, 1993; Williams-Linera and Herrera, 2003). However, in places with non-strong seasonality in water availability, percentages of leaf damage were relatively constant and lower throughout the year (Luquillo Experimental Forest, Puerto Rico; Angulo-Sandoval and Aide, 2000).

The wet-season seedlings were 12 weeks older when transplanted into the field than the dry-season ones. Since it has been reported that leaf age influences susceptibility to herbivores (Coley, 1983), it is possible that the lower rates of herbivory in the wet season and the absence of differences between abrupt and soft edge types in the wet season could be explained by increased toughness of mature leaves. We acknowledge that the design applied was limited, and our results must be interpreted cautiously, although in a previous study we found that leaf toughness supports postulated relationships between herbivory damage and plant defenses only partially (Williams-Linera and Baltazar, 2001).

Insect herbivory damage on oak seedlings was negatively correlated to air and soil humidity. In the same location, but in the forest interior, herbivory and insect herbivore abundance were positively correlated with soil water content (Williams-Linera and Herrera, 2003). Also, in a tropical lowland forest in Panama, Aide (1993) found the highest peak of herbivory (29.1%) when humidity was high and not during the dry season (23.1%). Similarly, other studies have documented how plant-insect herbivory varies in response to precipitation fluctuations in temperate upland oak forests (Shure *et al.*, 1998). Those authors documented that drought may operate indirectly on herbivore populations through their effects on plant foliar chemistry. Herbivory damage on oaks was reduced during the drought year (10%), and the extent of insect damage on oaks was significantly higher during the wet summer (13%).

Overall, the studied edge habitats present a microenvironmental gradient where air temperature in old-field and field edge is higher than in forest edge and forest interior, and relative humidity increases from the old-field to the forest interior. Several studies have reported similar microenvironmental changes along old-field–forest gradients (Williams-Linera *et al.*, 1998; Gehlhausen *et al.*,

## HERBIVORY AND EDGE EFFECT MODULATORS



**Figure 2.** Microenvironmental conditions in old-field–forest sites, Veracruz, Mexico. Air temperature (°C), soil temperature (°C), relative humidity (%) and soil water content (%) during the dry and the wet seasons in abrupt and soft edges (a, b, c, d), and in the abrupt and soft edges in old-field, field edge, forest edge and forest habitats (e, f, g, h). Error bars represent one S.E.

2000). However, general trends differed in intensity and depth penetration when different edge types were considered. In the abrupt edge, air temperature was higher whereas relative humidity and soil water content were lower because it represents a more exposed situation. The soft edge did not show an edge effect on air temperature, but displayed higher relative humidity and soil water content. In the old-field and forest edge, the soil was more humid along the soft edge.

When we compared herbivory in the dry season in soft

and abrupt edges, we detected that herbivory on *Quercus* was higher in the forest edge than at other locations from the border. Benítez-Malvido and Lemus-Albor (2005) found that leaf area damaged by herbivores was similar between forest interior and edges, but increased biotic damage in forest margins was due to pathogen damage. Similarly, in our study during the wet season, herbivory damage was similar at different distances from the border. Edge effect in forest fragments was obviously affected by surrounding vegetation structure. In this way, in the soft

edge, herbivory was lower than in the abrupt edge because humidity was higher along the gradient, and the abundance of plant growth near forest margins may attract insects by providing new food sources (Benítez-Malvido and Lemus-Albor, 2005). The secondary forest matrix may also allow for the free flux of herbivores present in successional vegetation to forest edges (Cadenasso and Pickett, 2000).

We conclude that herbivory damage on *Q. xalapensis* seedlings depends on several concomitant factors. Since the microenvironmental gradient depends on the edge contrast (abrupt *versus* soft edge), edge type affects microenvironment and herbivory. During the wet season humidity is similar in both edge types; therefore, insect herbivores can equally feed along the gradient. Although other factors such as light level and seedling density need to be incorporated in future studies, our preliminary conclusion for this study contributes to the edge theory as it underlines the importance of a temporal modulator factor for a higher or lower herbivory level inherently related to edge type.

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